The role of native marine predators in regulating invasions: a case-study of the invasive mussel *Semimytilus algosus* and native subtidal predators

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Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

The data pertaining to intertidal mussels in Chapter 1 was collected by Dr TB Robinson-Smythe.

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Abstract

In 2009 the Chilean mussel *Semimytilus algosus* was first recorded on the South African west coast and has spread extensively in this region. Current knowledge on this invasion is limited to intertidal habitats, leaving many unanswered questions regarding the subtidal distribution and abundance of this species and the implications of the invasion for subtidal communities. Predation is recognised as an important structuring force in subtidal communities and is thus one mechanism through which alien prey invasions can be regulated. However, knowledge is limited about when predator-driven biotic resistance may function effectively against alien prey. The overarching aims of this thesis were therefore to determine the subtidal status of *S. algosus*, to investigate the responses of native subtidal predators to this novel prey and ultimately to assess the drivers behind successful predator-driven biotic resistance in marine systems.

Semimytilus algosus was recorded at all sites between St. Helena Bay on the west coast and Seaforth on the south coast and its presence in the subtidal zone was quantified for the first time. Comparisons between intertidal and subtidal mussel communities revealed numerous differences. The long-established invasive mussel *Mytilus galloprovincialis* was virtually absent from subtidal communities despite its dominance in the intertidal zone. In contrast, subtidal communities were dominated by the native *Aulacomya atra*, followed by the native *Choromytilus meridionalis* and invasive *S. algosus*. Subtidal *S. algosus* reached sizes much greater than previously reported and had similar condition indices to native subtidal mussels. This suggests that this recent invader performs well in this habitat and is likely to continue to spread.

To investigate the potential for predator driven biotic resistance to the *S. algosus* invasion, the mussel prey preference of two native subtidal predators, the west coast rock lobster *Jasus lalandii* and spiny starfish *Marthasterias africana* was assessed. Despite being generalist predators, both displayed preference for native *C. meridionalis* over invasive *S. algosus*, even in cases when the latter was the most abundant prey. This finding was particularly unexpected as investigations into morphology and energetic content of the other mussel species highlighted that *S. algosus* represents the most energetically profitable prey with the highest energetic content while being the easiest for predators to access (i.e. has the thinnest shells and adductor muscles similar to the other mussel species).

Despite the clear results above, these represent outcomes of single predators whereas most natural communities contain multiple predators and prey selection may alter in the presence of competitors. However, the implications of multiple predator effects have rarely been considered in the context of alien prey invasions. Rock lobsters and whelks of the *Burnupena*

genus are predators known to co-occur within the invasive range of *S. algosus* in South Africa. Experiments revealed that when foraging in isolation, both predators preferentially consumed the native mussel *C. meridionalis*. However, when foraging together, the diet of *J. lalandii* became more varied, resulting in overall increased predation risk for the invasive *S. algosus.* Prey switching in *J. lalandii* is likely to reflect the lobsters attempting to minimise interactions with *Burnupena*, as high densities of these whelks represent a significant predatory threat to *J. lalandii*. These results highlight the need to account for multiple predators when assessing the potential impacts of native predators on alien prey.

Although predators currently appear to offer little resistance to the relatively new *S. algosus* invasion, the fact that prey preference can vary with exposure time to prey suggests that predators may increasingly incorporate this mussel in their diet with time. To test whether the lack of selection of *S. algosus* by *J. lalandii* can be overcome through continuous exposure to the invasive prey (i.e. conditioning), lobsters were fed solely on this species for four weeks. Subsequent assessments found that conditioned rock lobsters preferred *S. algosus* while displaying avoidance of the native mussels. This infers that biotic resistance potential can change over time and that native generalist predators may be able to adapt to an altered prey base and include invasive prey with time.

A literature review of predator-driven biotic resistance in marine systems revealed that the outcomes of interactions between native predators and alien prey depend on the characteristics of both trophic groups. Biotic resistance is typically effective when native predators are abundant, have high feeding rates, and when strong predation pressure is enforced on alien prey. Conversely, biotic resistance failure can be expected when any of these three predator characteristics are absent and when alien prey have high fecundity, high recruitment, and substantial dispersal potential. Thus, based on the characteristics of native subtidal predators and *S. algosus* as prey, it is unlikely that biotic resistance will be effective in the South African invasion. Overall, the results of this thesis demonstrate the complexity of predator-prey interactions in subtidal environments and that an increased understanding of the factors governing foraging behaviours can also improve our understanding of novel interactions between native predators and alien prey.

Table of Contents

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INTRODUCTION

Invasions by alien species represent a significant global threat to biodiversity (Anton et al. 2019), and rates of such events have increased notably over the last few decades (Clarke Murray et al. 2014; Ojaveer et al. 2018). These trends are expected to continue owing to the link between invasion and global trade and travel as well as climate change (Seebens et al. 2017; Ojaveer et al. 2018). It is now well-recognised that invasions by non-native species progress through a sequence: transport, introduction, establishment and spread (Blackburn et al. 2011). Different terms are used to refer to species as they progress through this sequence, and as a result there is some ambiguity in the literature regarding their usage (Colautti and MacIsaac 2004; Falk-Peterson et al. 2006). For clarity purposes, the terms related to the invasion status of species as they are used throughout this thesis are as in Robinson et al. (2016) (Table i).

Table i: Definitions of terms as used throughout this thesis (Robinson et al. 2016).

Term	Definition
Alien	Species whose presence in a given range is attributable to human actions that allowed them to overcome fundamental biogeographical barriers
Naturalised	Alien species that have self-replacing populations over several generations outside of captivity or culture, but that have not spread from their point of introduction
Invasive	Alien species that have self-replacing populations over several generations and have spread from their point of introduction

Biological impacts associated with alien species

The impacts assocaited with alien species can manifest at evolutionary and ecological levels (Grosholz 2002; Gallardo et al. 2016). Evolutionary impacts can include changes in the genotypes and phenotypes of native species. Genotypic changes, for example, can result following hybridization between native and invasive species and introgression of the invaders' genes into the native species gene pool (Huxel 1999; Grosholz 2002). A high degree of hybridization may threaten the future existence of native species. For example, in San Francisco Bay, California, hybridization between the invasive cordgrass *Spartina alterniflora* and the native *Spartina foliosa* has been extensive, with the majority of *Spartina* grasses in the bay now being hybrids and *S. foliosa* threatened with local extinction (Ayres et al. 2002).

Evolutionary impacts in the form of phenotypic changes can occur through adaptations in native species that relate to important life-history strategies. This can include changes in defence strategies, resource acquisition, reproduction, and any other adaptations that could enhance the persistence of a native species in an invaded habitat (Strauss et al. 2006). For example, the invasion of the freshwater golden apple snail *Pomacea maculata* has had

dramatic effects on the feeding landscape of a native predator, the snail kite *Rostrhamus sociabilis*, as the invader is significantly larger and has become more abundant than native apple snails. Snail kites depend strongly on apple snails as their main prey, with specialized bills that optimize feeding efficiency. A recent study shows, however, that snail kites have switched to feeding on the novel, more abundant *P. maculata,* with this switch being accompanied by an increase in bill size allowing it to predate upon the larger invasive prey (Cattau et al. 2018).

Ecological impacts of invasions are defined as significant and quantifiable alterations in the abundance and/or distribution of native species or habitats (Blackburn et al. 2014). This can occur through direct or indirect interactions between the invader and the invaded communities (Gallardo et al. 2016). Direct interactions include the formation of novel biotic interactions such as herbivory (Vermeij et al. 2009), parasitism (Torchin et al. 2002), competition (Mills et al. 2004; Berthon 2015), and predation (Pintor and Byers 2015; Holman et al. 2019). These novel interactions can produce community-level impacts, i.e. changes in broad measures such as native community diversity (Sadchatheeswaran et al. 2015; Gallardo et al. 2016). In marine systems, invasive predators have been shown to be capable of exerting impacts that span various trophic levels. Invasive predators with high feeding rates can cause notable declines in native prey populations (Ballew et al. 2016), which may lead to significant changes in native food webs (Arias-González et al. 2011). This has been demonstrated for a number of invasive marine predators, including lionfish *Pterois volitans* and *Pterois miles* (Albins and Hixon 2008; Ballew et al. 2016), the European shore crab *Carcinus maenas* (Walton et al. 2002; Ross et al. 2004), the Asian shore crab *Hemigrapsus sanguineus* (Lohrer and Whitlatch 2002), and the northern Pacific starfish *Asterias amerunsis* (Ross et al. 2004).

In addition to direct interactions between native and invasive species there are indirect interactions where the invader brings about changes in architectural habitat properties such as complexity or heterogeneity (Gallardo et al. 2016; Sadchatheeswaran et al. 2018) that will indirectly impact various native species. Organisms with this ability are referred to as ecosystem engineers, and examples of invasive ecosystem engineers include ascidians (Castilla et al. 2004), barnacles (Laird and Griffiths 2008; Gil and Pfaller 2016), oysters (Ruesink et al. 2005), and mussels (Robinson et al. 2007a; Sadchatheeswaran et al. 2015). In cases where ecosystem engineers decrease (or homogenize) habitat complexity, measures such as abundance and diversity have been observed to decrease. Conversely, these measures can be expected to increase when ecosystem engineering results in increased habitat complexity (Crooks 2002). More complex architectural structures may ameliorate some of the physical stressors facing native species and thereby increase the amount of suitable habitat (Wallentinus and Nyberg 2007; Sousa et al. 2009). However, not all native species will

benefit from such changes, and some may well be excluded from the community (Steffani and Branch 2005).

Factors determining invasion success in marine systems

Marine systems such as estuaries and coastal seas are regarded as some of the most heavily invaded ecosystems on earth (Castorani and Hovel 2016; Ojaveer et al. 2018) and even though the rates of introductions are expected to increase along with increases in human movement around the world, not all species that are introduced become successful invaders (Chan and Briski 2017). Developing a sound understanding of the factors that influence invasion success is of great importance as such knowledge can help to predict future invasions and their potential impacts and so enable their prevention.

In marine systems, there are various pathways through which alien species are introduced. These include shipping (Williams et al. 2013; Davidson et al. 2018), aquaculture (Naylor et al. 2001; Grosholz et al. 2015), the aquarium trade (Havel et al. 2015), canals (Galil et al. 2014, 2015), and oceanic rafting (Gil and Pfaller 2016; Simkanin et al. 2018). Once introduced, there are several key factors that can influence the success of an invasion. Even though such factors vary across different ecosystems, there is consensus in the literature that for most ecosystems, invasion success is strongly influenced by three main aspects: propagule pressure, and abiotic- and biotic conditions of the recipient environment (Catford et al. 2009; Gurevitch et al. 2011; Papacostas et al. 2017).

Propagule pressure can be defined as the number and frequency with which alien individuals are released into a non-native region (Lockwood et al. 2005). Strong propagule pressure (i.e. high numbers of individuals regularly released) is linked to increased chances of invasion success (Cassey et al. 2018) and can do so in several ways. It can increase the genetic diversity of the alien population thereby potentially increasing the adaptation capability to novel conditions in the introduced range (Lockwood et al. 2005). A persistent supply of propagules can also ensure that alien species are present if/when environmental conditions for establishment and spread transition from unfavourable to favourable (Lockwood et al. 2005). The degree to which propagule pressure affects marine invasions is not as well-studied as in terrestrial systems.This is largely due to the difficulties associated with experimental manipulations, detection and monitoring of alien propagules in the marine environment, and the strong publication bias toward terrestrial systems in the field of invasion biology (Pyšek et al. 2008; Johnston et al. 2009; Jeschke et al. 2012; Simkanin et al. 2017). However, existing literature on the topic suggests that propagule pressure operates synergistically with abiotic conditions such as habitat type (Simkanin et al. 2017). For example, areas exposed to high rates of shipping traffic, such as harbours, receive regular influxes of alien propagules resulting from hull fouling or ballast water exchange (Wasson et al. 2005). In addition to strong

propagule pressure, the abiotic conditions characteristic of harbours further act to promote invasion success. Most harbours are sheltered from strong wave action and consist predominantly of artificial structures (e.g. floating docks), both of which have been shown to favour the survival and establishment of alien species (Bulleri and Airoldi 2005; Dumont et al. 2011; Simkanin et al. 2012; Rogers et al. 2016). This combination of strong propagule pressure and favourable abiotic conditions have resulted in harbours being referred to as 'invasion hotspots' (Bulleri and Chapman 2010).

When estimates of propagule pressure are limited, information regarding abiotic conditions is often used to predict invasion success. The extent to which these conditions overlap between native and non-native regions is used to predict the environmental suitability of a non-native region, with a large degree of similarity often suggested to increase the chances of invasion success (Hayes and Barry 2008; Pyšek and Richardson 2010; Faulkner et al. 2014). Abiotic variables often considered in this way include temperature (Sanford et al. 2002; Canning-Clode et al. 2011), wave action (Robles et al. 2001), habitat complexity (Seitz et al. 2001; Griffen and Byers 2006) and salinity (Ashton et al. 2007). These predictions are often based on the realised niches of species in native ranges, i.e. their current observed distributions in relation to abiotic variables (Pearman et al. 2008). These niches can be a result of dispersal barriers and/or biotic interactions in the native range (Torchin et al. 2003; Mitchell et al. 2006). However, the fundamental niche, i.e. the true physiological tolerance of a species in relation to abiotic variables, may be much greater when constraints differ in the introduced region (Tingley et al. 2014). There could thus be mismatches between the predicted and observed niches of alien species. Examining biotic interactions in introduced ranges is one approach that can strengthen the accuracy of predictions regarding the potential ranges of alien species once they are introduced.

Biotic interactions, such as competition, herbivory, parasitism and predation, can play important roles in the outcomes of invasions. When studying these effects, it is important to note that the nature and impacts of these interactions on invasion success can vary geographically (Freestone et al. 2013) and has been demonstrated across latitudinal gradients. According to the biotic interactions hypothesis, interactions among tropical species should be stronger and more specialized than those in temperate regions, which increases species richness and diversification rates (Dobzhansky 1950). Stronger species interactions translate into stronger resource competition (Pianka 1966) and hence stronger biotic resistance (Elton 1958). Indeed, fewer marine invasive species are known from the tropics (Hewitt 2002). These predictions have been confirmed by Freestone et al. (2013), who demonstrated that biotic resistance, through predation in particular, is stronger in the tropics than in temperate zones. The impact of biotic interactions can further vary temporally (Diller et al. 2014; Cattau et al. 2018) as a result of unpredictable changes in native community composition. The

anthropogenic removal of keystone species (frequently predators) through overfishing can disrupt the interaction networks of native systems and thereby render them more vulnerable to invasions (Byers 2002a). The stability of native networks is also threatened by directional climate induced changes that can impact the performance (e.g. competitive abilities) of native species and its effects on invasions is currently of major concern (Occhipinti-Ambrogi 2007; Walther et al. 2009). Lastly, the impact of biotic interactions on invasion success can depend on the trophic levels involved (Kimbro et al. 2013). In marine systems, it has been shown that competition is most likely to affect invasions by alien consumers. Consumptive interactions (i.e. herbivory, predation), on the other hand, are more likely to impact alien producers (Kimbro et al. 2013).

The role of predator-prey interactions in regulating marine invasions

Predation is a well-recognised structuring force in marine environments (Connell 1961; Paine 1966), and changes in predator-prey interactions as a result of invasions can have wide-ranging impacts (Nicastro et al. 2007; Pintor and Byers 2015). The characteristics of native/invasive prey and predators underlie some of the main hypotheses that have been proposed to explain invasion success. Native predators may exert strong biotic resistance against invasive prey (DeRivera et al. 2005; Shinen et al. 2009) if the rate of consumption surpasses that of invasive prey reproduction (Twardochleb et al. 2012). However, due to a lack of coevolutionary history between native predators and novel invasive prey, it is not guaranteed that invasive prey will be recognised by native predators (Carlsson et al. 2009; Carthey and Blumstein 2018), and such prey may consequently escape predation. The enemy release hypothesis suggests that alien prey species may experience invasive success when they escape their natural predators and other enemies, provided that they are not consumed by native predators in the recipient region (Keane and Crawley 2002; Sih et al. 2010). It has also been suggested that organisms subjected to strong control by enemies in their native regions will have a higher potential to experience enemy release in introduced regions, with this effect most often observed in the context of marine invasions (Prior et al. 2015).

Following the release from enemies, alien species can divert the energy normally invested in enemy defence to other aspects of their life-history that may act to enhance invasiveness (Godoy et al. 2019). This is the mechanism suggested by the evolution of increased competitive ability hypothesis (Blossey and Nötzold 1995) with relevant characteristics most often relating to rates of growth and reproduction (Blossey and Nötzold 1995). Alien species might also possess defences that native enemies are not accustomed to and in this way can escape predation, as predicted by the novel weapons hypothesis (Callaway and Ridenour 2004). The successful invasion of Pacific red lionfish (*Pterois volitans* and *P. miles*) in the sub-tropical and tropical Western Atlantic and Caribbean has been linked to both enemy release and the use of novel weapons. These hyper-successful invaders flourish in

introduced ranges, as they are less susceptible to parasitic infections in these ranges and possess long venomous spines that serve as protection from novel predators (Albins and Hixon 2013; Tuttle et al. 2016).

Mussels as successful invaders

Some taxonomic groups have life-history strategies that predispose them to being successful invaders should they be introduced to novel regions. Mussels are one such group. Typically, mussel species that experience high invasion success share several key characteristics including the ability to reproduce and recruit in high numbers (Zeeman et al. 2018), grow rapidly (Branch and Steffani 2004) and thus achieve high abundances (Sousa et al. 2009, 2014). Examples of successful invasive mussel species with such characteristics include the golden mussel *Limnoperna fortunei* (Sylvester et al. 2007; Boltovskoy and Correa 2015), zebra and quagga mussels *Dreissena polymorpha* and *D. rostriformis* (Strayer 2009; Sousa et al. 2014; Marescaux et al. 2016) and the Mediterranean mussel *Mytilus galloprovincialis* (Apte et al. 2000; Lockwood and Somero 2011). All of these species have demonstrated ecological impacts attributable to their ecosystem engineering abilities (Sylvester et al. 2007) and have had major economic impacts through their effects on various industries including aquaculture (Connelly et al. 2007; Strayer et al. 2009; Boltovskoy and Correa 2015; Forrest and Atalah 2017).

Two invasive mussel species are present on the South African coastline. The first, *M. galloprovincialis*, is well-established along South African rocky shores (Assis et al. 2015). Native to the Mediterranean, and invasive in Namibia, Japan, Hong Kong and several locations on the northeast Pacifc coast (Apte et al. 2000; Wonham 2004; Robinson et al. 2005; Lockwood and Somero 2011), *M. galloprovincialis* was first recorded in the late 1970's in Saldanha Bay Harbour on the South African west coast (Grant and Cherry 1985). While the initial introduction was unintentional and thought to be related to shipping, regional spread was encouraged through translocation for mariculture purposes (Branch and Steffani 2004). This mussel has been well studied in the intertidal zone along this coast (Alexander et al. 2016) and therefore its impacts in this habitat are well understood. With a high physiological tolerance for desiccation, *M. galloprovincialis* has induced an upshore expansion of the width of intertidal mussel beds, and, on the west coast, has competitively displaced native mussels (*Aulacomya atra*, *Choromytilus meridionalis*) and a tube-building polychaete (*Gunnarea capensis*) (Hockey and van Erkom Schurink 1992; Branch et al. 2010; Sadchatheeswaran et al. 2015). In addition, *M. galloprovincialis* outcompetes the native limpets *Scutellastra granularis* and *S. argenvillei* for primary space, although juveniles of *S. granularis* gain additional recruitment substratum on the beds formed by *M. galloprovincialis* (Branch et al. 2010). As an ecosystem engineer, *M. galloprovincialis* has also driven significant changes in community structure and species diversity (Robinson et al. 2007a; Sadchatheeswaran et al. 2015).

Semimytilus algosus is the second mussel species to have invaded South African shores (de Greef et al. 2013). Native to Chile, *S. algosus* is gradually being recognised as a species with high invasive potential (Bigatti et al. 2014). Recent evidence suggests that *S. algosus* arrived on the South African west coast via larval dispersal from another invasive population in Namibia (Zeeman 2016). To date, *S. algosus* has established large intertidal populations along the west coast of the country (de Greef et al. 2013) and is spreading rapidly (TB Robinson unpublished data). In its native range, *S. algosus* is a strong competitor as demonstrated by its ability to form dense beds capable of excluding competitors (Tokeshi and Romero 1995; Bigatti et al. 2014). In South Africa, too, *S. algosus* has demonstrated this ability by excluding native primary space occupants, such as the limpet *S. granularis* and mussels *A. atra* and *C. meridionalis* (de Greef et al. 2013; Sadchatheeswaran et al. 2018). Similar to *M. galloprovincialis*, *S. algosus* has brought about significant changes in structural complexity on the west coast (Sadchatheeswaran et al. 2015). This species is reproductively active throughout the year (Navarrete et al. 2008; Reaugh-Flower et al. 2010) and has recently been shown to have exceptionally high rates of recruitment on the South African west coast (Zeeman et al. 2018). The high densities in which *S. algosus* settles have been suggested to represent an additional, abundant food source for native predators (de Greef et al. 2013), however, its role as a novel prey and the subsequent potential for predator-driven biotic resistance has not been investigated (but see Alexander et al. 2015a). This is a notable gap in knowledge as invasive prey, like *S. algosus*, can displace native prey and disrupt native food webs. If such organisms become numerically dominant and/or displace native prey, the feeding landscape of native predators may fundamentally change, resulting in alterations in feeding behaviours (Pereira et al. 2019). This can ultimately have important implications for both native predator and prey populations and existing food web dynamics. However, there is a global lack of understanding of the impacts of invasive prey in this context and it has been highlighted as an area in need of attention (Pintor and Byers 2015).

Thesis aims

The majority of research into mussel invasions along the South African coast has focussed on intertidal systems, likely due to the ease of monitoring and experimental manipulations in this zone. However, there is a major knowledge gap regarding the distribution, abundance and impacts of invasive mussels on predator-prey interactions in subtidal environments. Whilst intertidal communities are subjected to environmental stressors such as intense temperature fluctuations, desiccation and potentially strong wave action, subtidal communities experience more stable temperatures and are not threatened by the same stressors. In their absence, biological forces such as predation have increased potential to influence community composition in subtidal habitats (Gaymer et al. 2004).

Predation pressure from native predators may act to control populations of invasive prey (DeRivera et al. 2005). However, it is uncertain when such pressure can be expected to successfully regulate invasions by alien prey. Despite predictions that invasive mussels such as *S. algosus* may impact subtidal predators (de Greef et al. 2013), no studies have considered its subtidal distribution or abundance along the South African coastline nor its influence on the foraging of native predators.

In light of the above, the overarching aims of this thesis are to:

i. establish the subtidal status of the *S. algosus* invasion,
ii. investigate the foraging decisions of key subtidal predators when faced with mussel prey including the novel invasive prey *S. algosus*,
iii. explore if multiple predator effects shift mussel prey selection by a dominant subtidal predator and ultimately alter predation pressure on *S. algosus*,
iv. consider if avoidance of *S. algosus* can be overcome by conditioning of predators, and
v. assess the drivers of successful predator-driven biotic resistance in marine systems.

CHAPTER 1:

Semimytilus algosus in the subtidal zone: contrasts with intertidal patterns.

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Abstract

Two invasive mussel species are known from South Africa, *Mytilus galloprovincialis* and *Semimytilus algosus*. Most of the existing research on these invaders has focused on the intertidal zone, with little attention paid to subtidal habitats. This chapter addresses this knowledge gap by quantifying the relative abundance and size of native and alien mussels from the high-shore down to the subtidal zone, while accounting for the effects of wave exposure. In addition to these estimates, the condition of subtidal mussels was evaluated and compared across species. This was achieved through extensive surveys along the west coast of South Africa and the Cape Peninsula. At all shore zones, mussel abundance varied among species and wave exposures. In intertidal habitats, invasive species were recorded in greatest abundances at wave-exposed sites. Specifically, *M. galloprovincialis* was dominant on the high-shore, but this pattern changed down the shore. In the mid-shore, the invaders were equally dominant over native mussels, while on the low-shore *S. algosus* became the most abundant. Notably, the native *Choromytilus meridionalis* was absent intertidally. In the subtidal *M. galloprovincialis* was rarely present, while *S. algosus* maintained a strong presence. The maximum size of native *Aulacomya atra* and invasive *S. algosus* in the subtidal was roughly double that recorded in the intertidal zone. Subtidal *S. algosus* had condition similar to native mussels, further suggesting that the invader performs well in this habitat. Importantly, these results highlight that observations made from intertidal studies of mussel invasions cannot be used to infer subtidal patterns.

1.1 Introduction

The Mediterranean mussel *Mytilus galloprovincialis* is a dominant invasive species along the South African coast and occurs on rocky shores along approximately 2800 km of the coastline between Namibia and East London (Assis et al. 2015). The impacts of *M. galloprovincialis* in this habitat are well studied (Alexander et al. 2016), which is likely attributable to it having been present along this coast for more than 30 years (Grant and Cherry 1985). On the west coast, these impacts include partial competitive displacement of native biota such as limpets (Steffani and Branch 2005) and mussels (Sadchatheeswaran et al.

2015), as well as changing habitat structure and subsequent community composition through the creation of complex novel habitats (Robinson et al. 2007a; Sadchatheeswaran et al. 2015). On the south coast, partial habitat segregation between *M. galloprovincialis* and the native mussel *Perna perna* is maintained through differential recruitment patterns, post-settlement survival and adaptions to wave force (Zardi et al. 2008).

The Chilean mussel *Semimytilus algosus* was first detected on the west coast of South Africa in 2009 (de Greef et al. 2013). Recent evidence suggests that this species arrived on these shores through larval dispersal from the alien population in Namibia (Zeeman 2016). In its native range, *S. algosus* has strong ecosystem engineering abilities through formation of dense beds (Tokeshi and Romero 1995; Bigatti et al. 2014). In South Africa, *S. algosus* exerts similar impacts to *M. galloprovincialis*, through changes to community structure and species diversity (Sadchatheeswaran et al. 2015). Studies considering the distribution and spread of *S. algosus* along the South African coast are not as exhaustive as that of *M. galloprovincialis* (Robinson et al. 2005; Assis et al. 2015), likely reflecting the fact that the latter has been present along this coast for a much longer period of time. Nonetheless, as a species known to exert strong influences on rocky shore communities (Sadchatheeswaran et al. 2015), there is a need to monitor this invasion. The range of S. algosus in South Africa was documented as encompassing 500 km along the west coast in 2010 (de Greef et al. 2013) and in 2015 the prediction was made that, if *S. algosus* were to reach the south coast, the species would likely become established (Alexander et al. 2015b). Since then such a range expansion onto the south coast has been documented (TB Robinson unpublished data).

In the intertidal zone, *S. algosus* has been recorded in highest abundance on the low-shore, while *M. galloprovincialis* dominates the mid- to high-shore (de Greef et al. 2013). However, there is a large gap in knowledge regarding the dynamics of subtidal mussel populations, and whether the invasive *M. galloprovincialis* and *S. algosus* are dominant in this habitat, as they are in the intertidal zone. In intertidal habitats, the upper distributions of sessile species are determined predominantly by their physiological tolerances to desiccation, heat stress, and wave exposure (Zardi et al. 2008; Erlandsson et al. 2011); while biotic interactions such as competition and predation become increasingly important low on the shore (Connell 1972; Menge 2002). However, factors such as desiccation and heat stress become irrelevant when organisms are permanently submerged and exposed to stable temperatures. Nonetheless, water movement remains as an important structuring force (Westerbom and Jattu 2006; von der Meden et al. 2008) and species occupying sites characterised by a high degree of water movement will require a stronger attachment strength compared to those that inhabit more sheltered sites (Steffani and Branch 2003a; von der Meden et al. 2008). Utilisation of resources such as food and space are also key determinants of subtidal mussel communities. Food intake in turn influences growth and reproduction (Xavier et al. 2007), and

surplus energy can be invested into the production of byssus threads, shells and body tissues (Steffani and Branch 2003a).

Despite the knowledge base on the distribution and abundance of mussels within the intertidal zones of large sections of the South African west and south coasts (van Erkom Schurink and Griffiths 1993; Rius and McQuaid 2006; Branch et al. 2008; Erlandsson et al. 2011), information is presently lacking for subtidal habitats. Thus this chapter aimed to quantify and compare the abundance and size of intertidal and subtidal mussel species within the range shared by *M. galloprovincialis* and *S. algosus*. Based on intertidal trends, it was hypothesized that (1) the invasive mussels *M. galloprovincialis* and *S. algosus* would support populations in the subtidal zone, and (2) that the densities of invasive mussels would be greater than those of native mussels (*A. atra* and *C. meridionalis*) in both intertidal and subtidal communities. As the condition of mussels can provide insight into their performance in a particular habitat, this measure was also quantified for all subtidal mussel species.

1.2 Methodology

Intertidal and subtidal surveys were carried out in winter of 2016 along the west coast and Cape Peninsula, South Africa (Fig. 1.1). Sites were chosen to cover the shared range of the two invasive mussels *Mytilus galloprovincialis* and *Semimytilus algosus*, and to include sites exposed to different wave forces, i.e. sheltered (n = 2), semi-exposed (n = 2), and exposed sites (n = 2) (following Steffani and Branch 2003a).

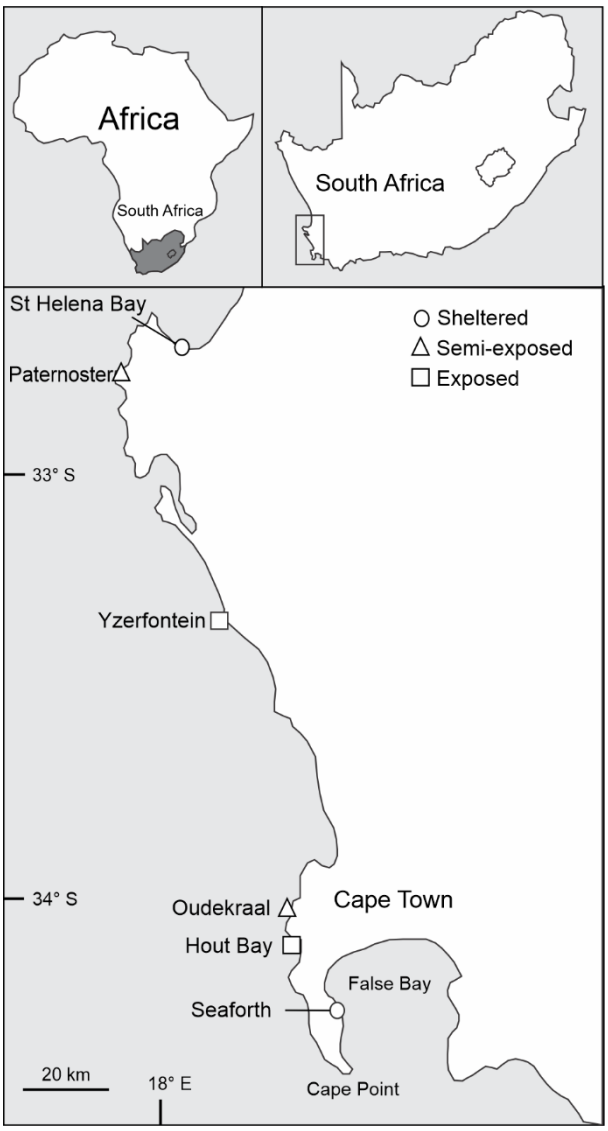

Figure 1.1: Sites where intertidal and subtidal mussel surveys were conducted. These sites were characterised as sheltered (circles; St Helena Bay, Seaforth), semi-exposed (triangles; Paternoster, Oudekraal), or exposed (squares; Yzerfontein, Hout Bay).

At all sites, five 20 x 20 cm quadrat samples, separated by 1 – 10 m, were collected from each of the high-, mid-, and low-shore zones. All mussels present were identified to species level and counted. At each site, 50 individuals per species were measured unless fewer individuals were detected. Subtidal surveys were conducted by divers. Surveys comprised four 50 m transects that were swum perpendicular to the shore in search of mussels. Along each transect, five quadrats (20 x 20 cm) were scraped from mussel beds and the samples returned to the laboratory where all mussels were identified to species level and individuals counted and measured.

Condition of subtidal mussels

The condition of mussels is a characteristic influenced by the rate and efficiency of food intake and thus represents a measure of performance in a particular environment (Steffani and Branch 2003a). This measure has not yet been quantified for subtidal mussels along the South African west and south coasts and was thus done in this study. Condition indices were derived for 50 adult individuals per species per site unless fewer individuals were detected. In the laboratory, flesh and shells of mussels were separated and weighed to the nearest 0.01 g. These were then oven-dried at 80˚C until they reached a constant weight. The condition of mussels is defined as the relationship between dry flesh and shell weight and can be used to calculate the condition index (CI) as follows (Davenport and Chen 1987):

$$\mathrm{CI} = \left(\frac{\text{Dry flesh mass (mg)}}{\text{Dry shell mass (mg)}}\right) * 100$$

Statistical analyses

As assumptions of normality and equal variances were met, comparisons of mussel abundance among species (*A. atra*, *C. meridionalis*, *M. galloprovincialis* and *S. algosus*) and wave exposure levels (sheltered, semi-exposed, and exposed) were made using a two-way ANOVA followed by Tukey HSD post hoc tests. Separate analyses were undertaken for each shore zone, including the subtidal zone. Mussels were absent from the intertidal on sheltered shores. As such, comparisons of abundance among species in the intertidal zone included only semi-exposed and exposed conditions. For each species, size was compared between intertidal and subtidal populations using a Mann-Whitney test as the data were not normally distributed. Additionally, Kolmogorov-Smirnov tests were used to compare size-frequency distributions of intertidal and subtidal mussels. Comparisons of condition indices were also made using a two-way ANOVA that considered subtidal mussel species (*A. atra, C. meridionalis, S. algosus*) and wave exposure levels (sheltered, semi-exposed, exposed). All analyses were carried out in RStudio (R Development Core Team 2016).

1.3 Results

Mussel abundance

Semimytilus algosus was found to be present at all intertidal and subtidal sites. Mussel abundance differed significantly among species and wave exposures, regardless of the shore zone considered (Table 1.1), with significant interactions between these factors.

Table 1.1: Results from two-way ANOVAs comparing mussel abundance among species (*Aulacomya atra*, *Choromytilus meridionalis, Mytilus galloprovincialis, Semimytilus algosus*) and wave exposure levels (sheltered, semi-exposed, exposed) in the high-, mid- and low-shore as well as the subtidal zone.

	Factor		
Shore zone	**Species**	**Exposure**	**Species*Exposure**
High-shore	$F_{2, 45} = 33.43$, $p < 0.001$	$F_{1, 45} = 17.92$, $p < 0.001$	$F_{1, 45} = 16.4$, $p < 0.001$
Mid-shore	$F_{2, 54} = 104.4$, $p < 0.001$	$F_{1, 54} = 149.02$, $p < 0.001$	$F_{2, 54} = 35.57$, $p < 0.001$
Low-shore	$F_{2, 72} = 101.57$, $p < 0.001$	$F_{1, 72} = 145.69$, $p < 0.001$	$F_{3, 72} = 55.37$, $p < 0.001$
Subtidal	$F_{2, 306} = 5.536$, $p = 0.004$	$F_{2, 306} = 5.306$, $p = 0.005$	$F_{4, 306} = 4.879$, $p < 0.001$

In the high-shore of exposed and semi-exposed sites, invasive *Mytilus galloprovincialis* was the most abundant species (Fig. 1.2). Both invasive species (*M. galloprovincialis* and *Semimytilus algosus*) reached highest abundance on the mid- and low-shore zones of exposed sites (Fig. 1.2). At all sites, *M. galloprovincialis* and *S. algosus* were significantly more abundant than native species on the mid-shore, whereas *S. algosus* outnumbered native species on the low-shore (all sites). The native mussel *Choromytilus meridionalis* was absent from the high- and mid-shore, and first appeared in the low-shore, increasing in abundance in the subtidal, with the highest subtidal numbers of this species recorded at sheltered and exposed sites (Fig. 1.2). Very low numbers of *M. galloprovincialis* were recorded in the subtidal, with only a few individuals recorded from a single exposed site (Hout Bay). In contrast, the recent invader *S. algosus* supported large populations in the subtidal, with highest numbers recorded at sheltered and exposed sites.

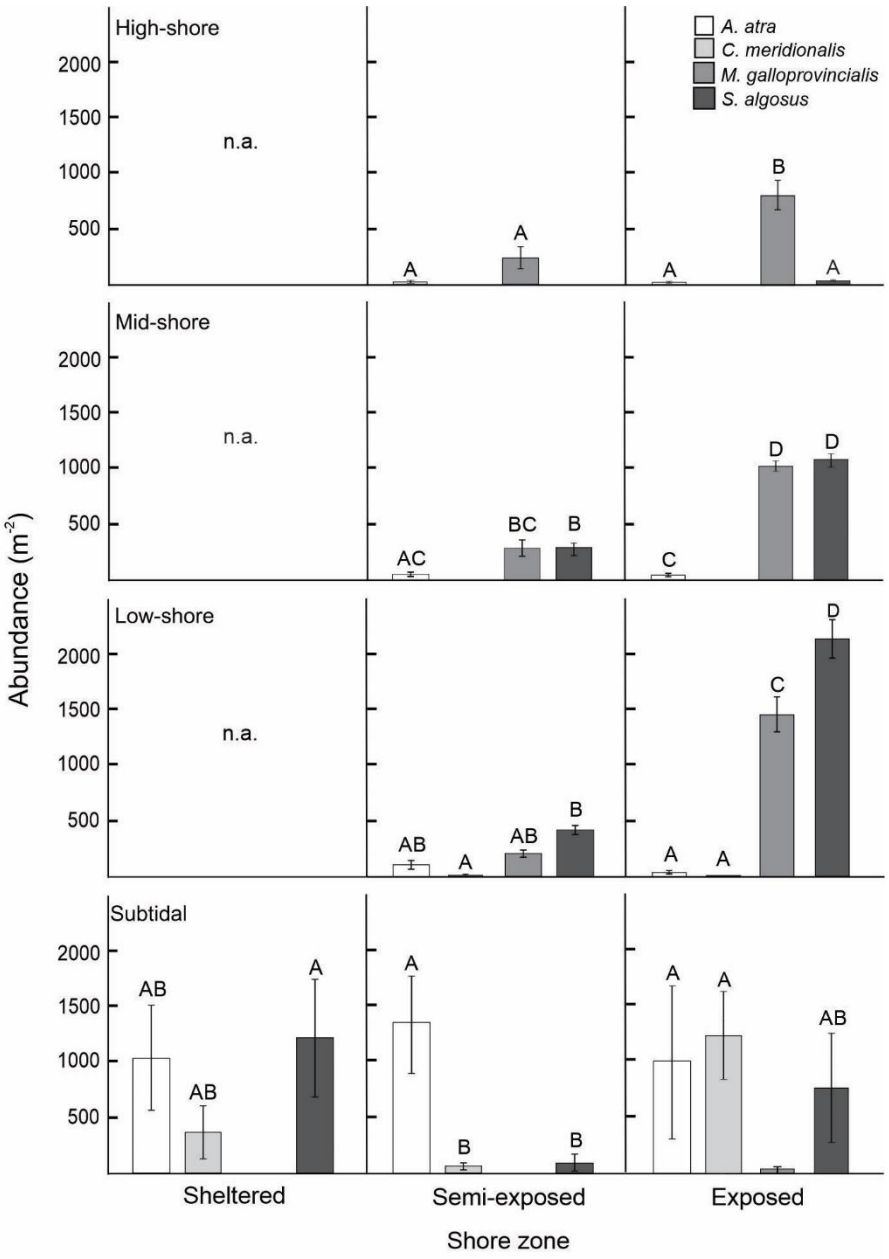

Figure 1.2: Abundance (mean ± SE) of native (*Aulacomya atra*, *Choromytilus meridionalis*) and invasive (*Mytilus galloprovincialis*, *Semimytilus algosus*) mussels in various shore zones (high-shore, mid-shore, low-shore, subtidal) on sheltered, semi-exposed, and exposed shores. The absence of mussels from intertidal shore zones of sheltered sites is denoted by 'n.a'. Shared letters above bars indicate no significant difference (Tukey's HSD post-hoc test, $p < 0.05$). *Mytilus galloprovincialis* was not included in comparisons for the subtidal zone as it only occurred at a single exposed site.

Mussel size

Mann-Whitney tests showed a significant difference in the sizes of intertidal and subtidal *Aulacomya atra* ($U = 541080$, $p < 0.001$) and *S. algosus* ($U = 146430$, $p < 0.001$) (Fig. 1.3). Kolmogorov-Smirnov tests revealed a significant difference between the size frequency distributions of intertidal and subtidal populations of these species (*A. atra* $D = 0.408$, $p <$

0.001; and *S. algosus* D = 0.225, p < 0.001). For both species, intertidal populations supported smaller mussels while larger mussels were found in subtidal populations. The intertidal size range of *A. atra* was 2 – 48 mm, while subtidal conspecifics ranged from 1 – 90 mm. *Semimytilus algosus* ranged from 3 – 54 mm in the intertidal, and from 1 – 128 mm in the subtidal. The absence of *C. meridionalis* and *M. galloprovincialis* from intertidal and subtidal sites, respectively, precluded comparisons between these habitats.

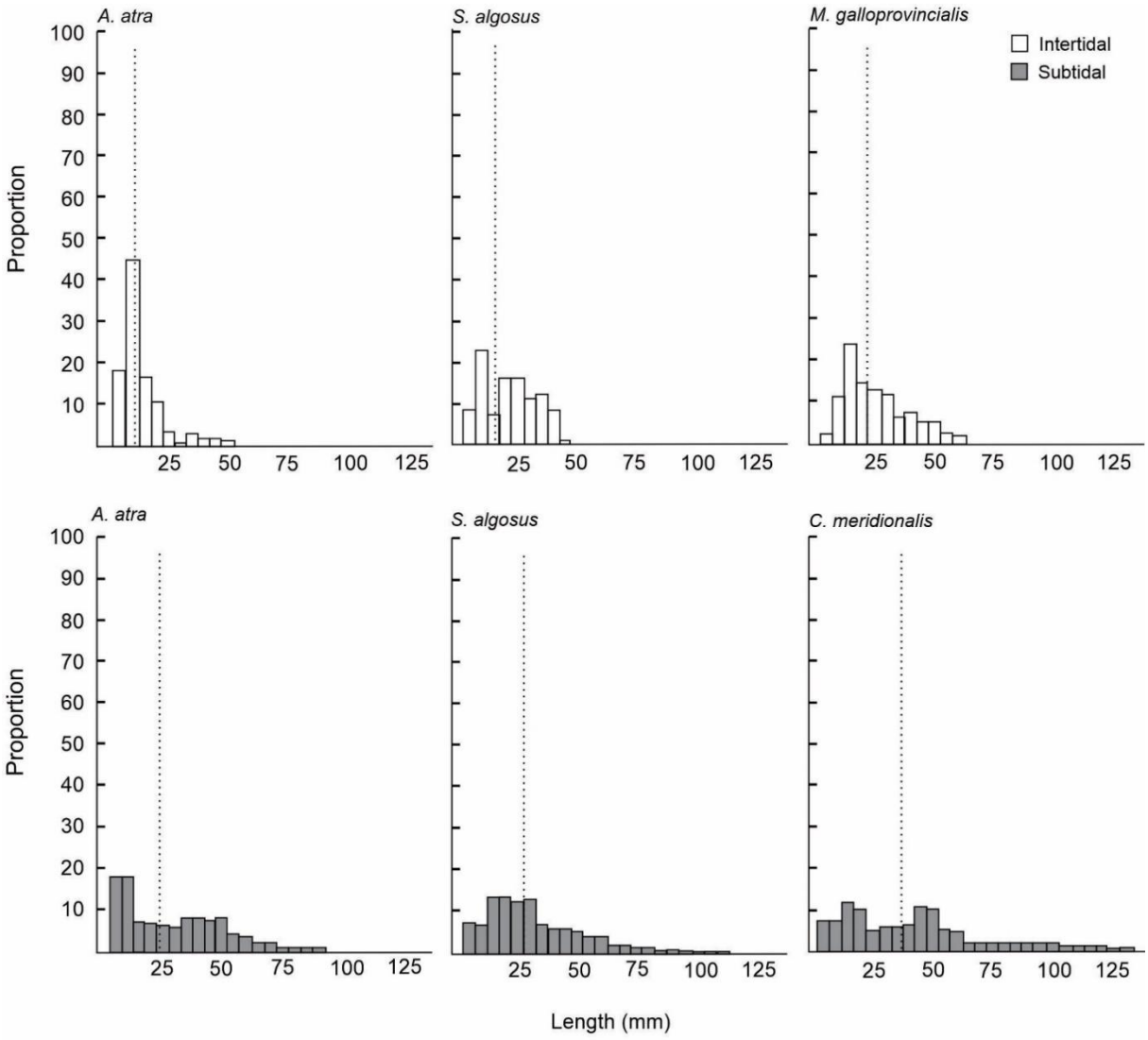

Figure 1.3: Proportional size-frequency distributions of intertidal (white bars) and subtidal mussels (grey bars). Medians are represented by dotted lines. It was not possible to construct meaningful size-frequency distributions for subtidal *Mytilus galloprovincialis* and intertidal *Choromytilus meridionalis* as fewer than 50 individuals of these species were present in these respective habitats. As such, size-frequency distributions for only intertidal *M. galloprovincialis* and subtidal *C. meridionalis* are shown.

Condition of subtidal mussels

The two-way ANOVA comparing condition among the three subtidal species (*A. atra, C. meridionalis*, *S. algosus*) and wave exposure levels (sheltered, semi-exposed, exposed)

revealed no significant difference among species ($F_{2, 645}$ = 0.170, p = 0.843), but a significant difference in mussel condition among wave exposure levels ($F_{2, 645}$ = 267.131, p < 0.001) (Fig. 1.4). The interaction between wave exposure level and mussel species was also significant ($F_{4, 645}$ = 6.155, p < 0.001). Subtidal mussels at sheltered sites had the highest condition (17.4 ± 4.12, mean ± SD), following by those on exposed (12.28 ± 3.28) and semi-exposed (9.25 ± 2.8) shores (Fig. 1.4).

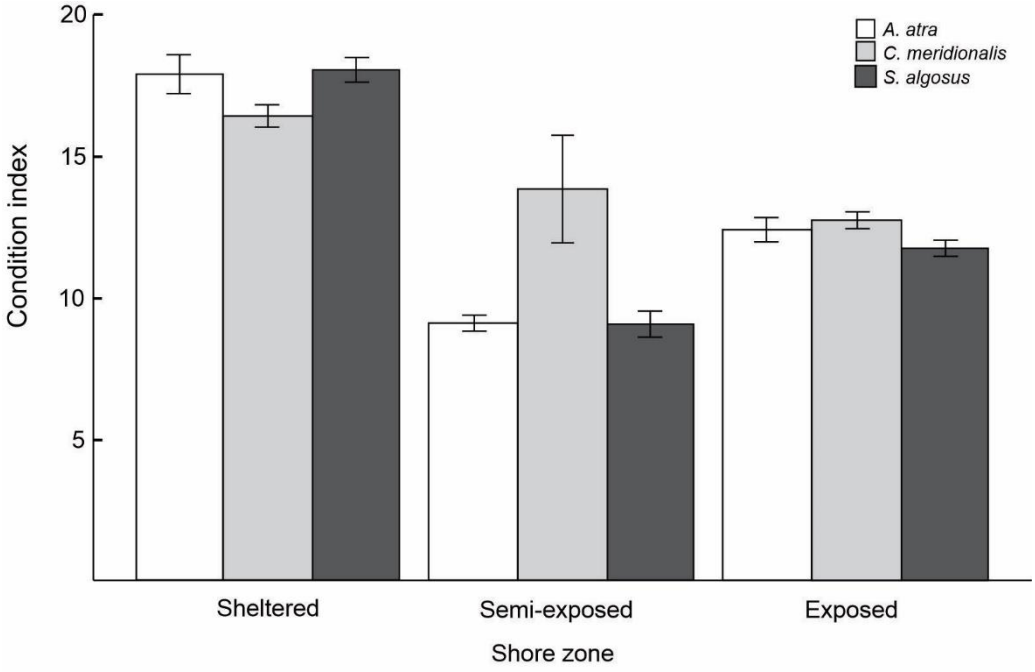

Figure 1.4: Mean (±SE) condition indices of three subtidal mussel species (*Aulacomya atra, Choromytilus meridionalis*, *Semimytilus algosus*) at sites characterised by different wave exposure levels (sheltered, semi-exposed, exposed).

1.4 Discussion

Invasive mussels supported greater densities than native mussels in intertidal communities, although this did not hold for the subtidal zone. In subtidal communities, native mussels were more abundant than intertidal conspecifics, and invasive *Semimytilus algosus* was present at densities comparable to native species. In contrast to intertidal communities, *Mytilus galloprovincialis* was the least abundant species in the subtidal zone. In intertidal habitats in the high-, mid- and low-shore, exposed sites supported a greater abundance of mussels than semi-exposed and sheltered sites, with no mussels present in the latter. While it is important to acknowledge that the sheltered sites in this study fell within St. Helena Bay (an area well known for low oxygen conditions (Lamont et al. 2015)) and along the Cape Peninsular in False Bay (which is adjacent to the biogeographic breakpoint that separates the south and west coasts (Sink et al. 2012)), and that these two sheltered sites were the only sites to fall downstream of upwelling centres (Pfaff et al. 2011), the results obtained are considered a valid

representation of sheltered shores. This is because (1) low oxygen conditions are focused in the bottom waters of St. Helena Bay, with wind driven mixing ventilating waters in the nearshore where this study was conducted (Lamont et al. 2015); (2) a previous study has demonstrated that mussels respond similarly to wave action along the Cape Peninsula as they do further up the west coast (Steffani and Branch 2003a); (3) intertidal recruitment of mussels is known to be greater downstream of upwelling centres (Pfaff et al. 2011) which suggests that if this factor affected our findings we should have recorded elevated abundances of mussels at our sheltered sites rather than their absence; and (4) the absence of mussels at sheltered sites has previously been documented along this coast (Steffani and Branch 2003b). Numerous studies considering the role of wave action have demonstrated its importance in determining the distribution and co-existence of sessile marine species. For example, it has been shown that *M. galloprovincialis* reaches highest abundance in exposed sites (Branch et al. 2008), and that growth and condition index are highest on these shores (Steffani and Branch 2003a). It has been suggested that this is driven by an elevated food supply on more exposed shores resulting from greater water movement (Steffani and Branch 2005), and that the overall scarcity of mussels on sheltered shores is likely a result of an insufficient food supply for filter feeders such as mussels (Steffani and Branch 2003a). The condition of subtidal mussels did not differ among species, although mussels in sheltered sites had higher condition than those in semi-exposed and exposed sites.

The numerical dominance of *M. galloprovincialis* in the high- and mid-shore zones is supported by previous research (Branch and Steffani 2004; de Greef et al. 2013) and is most likely attributable to the high desiccation tolerance, high recruitment rates, and low tolerance to inundation by sand (van Erkom Schurink and Griffiths 1991; Hockey and van Erkom Schurink 1992; Zardi et al. 2008). In intertidal rocky shore communities on the west coast, the competitive superiority of *M. galloprovincialis* has been suggested to be an important driver of the decline of native *Aulacomya atra* (Robinson et al. 2007a), and the overall scarcity of *Choromytilus meridionalis* (Sadchatheeswaran et al. 2015). However, with decreasing tidal elevation the abundance of *M. galloprovincialis* also decreased, with only a few individuals recorded at a single, exposed subtidal site (Hout Bay). This is surprising, especially considering the fact that this species is farmed subtidally in Saldanha Bay (Probyn et al. 2001). While the subtidal scarcity of *M. galloprovincialis* remains unclear, future studies could consider the settlement and survival rates of subtidal *M. galloprovincialis* recruits, and/or the attachment strength of subtidal *M. galloprovincialis* compared to co-occurring mussel species in this zone.

Semimytilus algosus exhibited a strong presence in inter- and subtidal mussel communities. In its native range in Chile, *S. algosus* is the competitive subordinate of *Perumytilus purpuratus* in intertidal habitats but can nonetheless be found at most sites on the

mid to low shore (Navarrete et al. 2008). However, *S. algosus* is known to also occur subtidally, while *P. purpuratus* is restricted to the intertidal zone (Navarrete et al. 2015). On the South African coastline, *S. algosus* outnumbered all co-occurring mussel species on the low shore and native species in the mid shore. The discrepancy in dominance status of *S. algosus* between Chile and South Africa could be due to differences in recruitment patterns. South African mussels exhibit seasonal peaks in recruitment whereas recruitment of Chilean mussels (*S. algosus* and *P. purpuratus*) occurs throughout the year (Navarrete et al. 2015; Zeeman et al. 2018). Unlike *M. galloprovincialis*, *S. algosus* reached high abundances subtidally, suggesting that it performs as well as native species in subtidal habitats. Notably, *S. algosus* was recorded in high numbers in intertidal and subtidal habitats at the edge of its current eastward distribution and, as such, monitoring of this species is recommended.

The large size reached by *S. algosus* and *A. atra* in the subtidal compared to intertidal conspecifics is notable. Subtidally, *S. algosus* reached maximum sizes larger than 120 mm, in contrast to 54 mm in the intertidal. This is particularly surprising, as previous studies report that the maximum size of this species does not exceed 60 mm (de Greef et al. 2013). This is notable as the perceived small size of this species has underpinned the notion that *S. algosus* would remain within a window of vulnerability (5 – 60 mm) for mussel predators (de Greef et al. 2013). It is probable that the discrepancy in size between intertidal and subtidal habitats is the result of constant food supply for mussels in the latter (Westerbom and Jattu 2006). The scarcity of large mussels in intertidal zones is unlikely to be a result of selective harvesting, as the sites surveyed are not frequented by mussel harvesters. As such, it is suggested that while intertidal populations of *S. algosus* remain vulnerable to mussel predators, subtidal conspecifics may face reduced susceptibility due to their increased size. This has important implications for the future invasion of *S. algosus* as large mussels contribute proportionally more to the reproductive output of the population (van Erkom Schurink and Griffiths 1991; Xavier et al. 2007) and can thus contribute to the spread of this invader. It would be useful for future studies to examine the mechanisms responsible for the size differences between inter- and subtidal mussels. For example, intertidal mussels might be facing trade-offs between energy invested in growth versus energy invested in attachment strength/desiccation tolerance, while subtidal mussels may invest more energy in growth as they are not exposed to the same environmental stressors as intertidal mussels. Lastly, the invasive success of *S. algosus* in the subtidal is demonstrated by this species having similar condition than native mussels. High condition of mussels in sheltered sites could be due to differences in energy allocation. Mussels in more exposed sites are thought to invest more energy toward protection from dislodgment (e.g. stronger byssus threads) than flesh production (Steffani and Branch 2003a). Although there are no studies that examine this in subtidal mussels, it has been suggested that intertidal mussels allocate more energy to the production of byssus threads when they are exposed to stronger wave action (Young 1985). Lower condition might also be

a result of energy rather directed towards shell growth, which could be reflective of an anti-predation strategy and/or to generate a larger reproductive output (Xavier et al. 2007). There is a lack of research on the drivers of condition in subtidal mussels and as such, the reasons behind the observed differences remain unclear.

In conclusion, the high densities supported by the invasive mussels *M. galloprovincialis* and *S. algosus* in the intertidal zone are not mirrored in the subtidal. Rather *M. galloprovincialis* is almost absent from natural subtidal habitats. Despite the relatively short timeframe that *S. algosus* has been present on South African shores, it has become a dominant invader both intertidally and subtidally. As *S. algosus* has been shown capable of forming dominant invasive populations, displacing native biota and significantly altering native community structures (de Greef et al. 2013; Sadchatheeswaran et al. 2015), it is recommended that monitoring of this incursion be undertaken in both intertidal and subtidal habitats.

CHAPTER 2:

Impacts of the *Semimytilus algosus* invasion on the prey preference of the native west coast rock lobster *Jasus lalandii* and the spiny starfish *Marthasterias africana*

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Abstract

Invasions by alien prey can lead to the displacement of native prey species and thereby change the foraging landscape of native predators. This chapter investigated the prey preference of two native mussel predators, the west coast rock lobster *Jasus lalandii* and the spiny starfish *Marthasterias africana*, when exposed to varying combinations of native (*Aulacomya atra*, *Choromytilus meridionals*) and invasive (*Mytilus galloprovincialis*, *Semimytilus algosus*) mussels. Given the generalist feeding nature of lobsters and starfish and the notion that their diets reflect prey availability, it was predicted that they would consume the most abundant prey, regardless of native or invasive status. Laboratory experiments were conducted where each predator was presented with mussel species in relative densities that represented pre- and post-invasion scenarios (with respect to the *S. algosus* invasion). In addition, the shell strength, adductor muscle strength, and energetic content of the four mussel species was determined as these parameters may be of importance in explaining prey selection by the predators. It was found that both predators preferred the native *C. meridionalis*, even when it was the least abundant prey. This is surprising, especially as the mussel parameters suggested invasive species would be easier to consume. These findings demonstrate that native predators may reduce the competition faced by invasive species by preferentially consuming their native comparators, thereby leading to the potential facilitation of the invasion.

2.1 Introduction

Native predator-prey relationships have, in most cases, co-evolved over extensive periods of time (Carlsson et al. 2009) and the arrival of a novel prey or predator can disrupt these relationships and potentially result in unstable predatory interactions. For example, in the Caribbean the invasion of lionfish (*Pterois volitans, Pterois miles*) has impacted native coral reef fishes (Albins and Hixon 2008) and is responsible for major reductions in recruitment of these fish (Albins and Hixon 2013). These prey share no co-evolutionary history with lionfish and are thus ill-equipped to effectively avoid or defend themselves against this novel predator.

In some instances, native prey may develop defences against novel invasive predators after being exposed to them for a certain time period (Freeman and Byers 2006). In its native North American range, populations of the mussel *Mytilus edulis* that have been exposed to a novel crab predator (*Hemigrapsus sanguineus*) for several generations have shown induced shell thickening in response to predatory cues from *H. sanguineus*. In contrast, *M edulis* populations that occur outside of the invasive range of *H. sanguineus* fail to display any detection of these predatory cues and subsequent morphological anti-predator adaptation (Freeman and Byers 2006).

The majority of invasion biology research on novel predator-prey interactions has focussed on the impacts of invasive predators rather than invasive prey, probably because the impacts of invasive predators being perceived to be far more damaging than those of invasive prey (Salo et al. 2007). However, there is a growing awareness of the role that invasive prey species may have in native systems (Carlsson et al. 2009). Invasive prey often establish in large numbers (Sousa et al. 2009), with the potential to competitively displace native prey (Sadchatheeswaran et al. 2015). Invasive prey may present a novel food source that, if in high enough abundance, could induce a predatory switch in the prey selection by native predators (Sousa et al. 2009). For example, the invasion of Lake Erie by round gobies (*Neogobius melanostomus*) induced a shift in the prey preference of the native and endangered Lake Erie Water Snake (*Nerodia sipedon insularum*), a phenomenon attributed to the high abundance of this novel prey (King et al. 2006). In this scenario, the shift towards invasive prey had positive outcomes for Water Snakes, resulting in faster growth rates and larger body sizes for the native predator. Indeed, it has been suggested that the overall outcome of this predatory switch might counteract some of the pressures that threaten the Water Snake in this system (King et al. 2006).

There are instances where a switch towards invasive prey selection can invoke biotic resistance by the native predators (García and Protogino 2005; Sousa et al. 2009; Carlsson et al. 2011; Freestone et al. 2013) which can in turn act to limit the abundance and distribution of invasive prey (MacNeil et al. 2013). However, these prey switches to novel invasive prey might not be straightforward or indeed feasible, and native predators may fail to recognize novel invasive prey organisms as an additional food source (Robinson et al. 2015; Hostert et al. 2018). When native predators continue to consume native prey, it may facilitate invasions of the alien prey by removing native competitors (Needles et al. 2015) and releasing the alien prey from the predatory pressures normally experienced in its native range (as per the enemy release hypothesis, Colautti et al. 2004). These effects can ultimately act to increase the chances of a successful invasion. When invasive prey become more abundant than native prey, predators that are unable to switch toward abundant invasive prey may also experience decreased fitness (e.g. in the form of reduced body condition or growth) compared to those

that are able to feed easily on the novel prey (Carlsson et al. 2009). Switching from familiar to novel prey has been suggested to occur in generalist predators (Jaworski et al. 2013). Although clear definitions of generalists versus specialists are illusive (Futuyma and Moreno 1988; Vamosi et al. 2014), in the context of predators, generalists are most often categorized based on their consumption of a variety of prey species that can differ morphologically (for example see Hughes and O'brien 2001; Finlay-Doney and Walter 2012; Gianguzza et al. 2016). This characterisation was applied in this chapter.

In South Africa, invasions by the mussels *Mytilus galloprovincialis* (Grant and Cherry 1985) and *Semimytilus algosus* (de Greef et al. 2013) have occurred at the expense of native mussels *Aulacomya atra* and *Choromytilus meridionalis*, resulting in the displacement of these species along many stretches of coastline (Sadchatheeswaran et al. 2018). Mussels represent an important food source for various intertidal and subtidal predators including whelks, marine birds, starfish and rock lobsters (Griffiths and Hockey 1987; Caro et al. 2008; Alexander et al. 2015a). As such, it has been suggested that the abundant invasive mussels *M. galloprovincialis* and *S. algosus* could represent a new food source for native marine predators (de Greef et al. 2013). Indeed, the African Black Oystercatcher *Haematopus moquini* has undergone a dietary switch toward *M. galloprovincialis*, which led to an increase in the reproductive potential of these birds and a change in their conservation status from Endangered to Near Threatened (Coleman and Hockey 2008). The native predatory whelk *Trochia cingulata* has undergone a similar change, with a shift in feeding towards *M. galloprovincialis* and the morphologically similar *S. algosus* (Alexander et al. 2015a). However, knowledge of the impacts of these mussel invasions on subtidal predators is lacking and, given a recent range expansion of *S. algosus* onto the south coast (Chapter 1), it becomes important to determine how subtidal predators in this extended range will respond to this novel prey.

Two important subtidal predators within the invasive range of these mussels are the west coast rock lobster *Jasus lalandii* and the spiny starfish *Marthasterias africana* (previously misidentified as the European species *M. glacialis*; Wright et al. 2016). Rock lobsters are considered to have an important role in the structuring of subtidal communities through predation (Robles et al. 1990; Mayfield et al. 2000a; Blamey and Branch 2012). The predatory force exerted by *J. lalandii* is of such magnitude that this species is considered the driving force behind two alternative stable states in the subtidal communities of two South African west coast islands (Barkai and Branch 1988a). Rock lobsters consume a variety of protein-rich organisms including whelks, limpets, fish, urchins, sponges, mussels and conspecifics (Mayfield et al. 2000a; Mayfield and Branch 2000; Haley et al. 2011). Although *J. lalandii* can consume a variety of prey, it has been shown to exhibit a distinct preference toward sea urchins and mussels (Mayfield and Branch 2000). While there is evidence of *J. lalandii* consuming the invasive mussel *M. galloprovincialis* (Nicastro et al. 2007), no studies have considered if *S.*

algosus has been incorporated into its diet and/or whether this has an effect on the selection of prey.

Starfish are similarly considered important benthic predators that have impact at a variety of scales, shaping populations and assemblages within their respective communities (Verling et al. 2003; Himmelman et al. 2005). Locating resources through chemoreception (Nadaeu et al. 2009), they feed mostly on sessile or slow-moving prey (Himmelman et al. 2005). In South Africa, the native starfish *M. africana* has been shown to exhibit a preference toward mussels (Branch 1978; Penney and Griffiths 1984). Although it is recognised that species in this genus can exert strong predation pressure on prey populations (Verling et al. 2003), it has not been the subject of much research, especially in South Africa. To date, the majority of studies have focussed on the importance of starfish predation on intertidal communities despite the fact that their impact is thought to be most evident in subtidal systems (Gaymer et al. 2004).

Previous research has described rock lobsters and starfish as generalist predators (Penney and Griffiths 1984; Mayfield et al. 2000a; Verling et al. 2003), based on their tendency to feed on a variety of prey (e.g. mussels, winkles, sea urchins, fish, limpets, whelks, barnacles, algae, and sponges; Penney and Griffiths 1984; Mayfield et al. 2000a; Mayfield and Branch 2000), with their diets often reflective of prey availability (Menge 1972; Penney and Griffiths 1984; Mayfield et al. 2000b; Navarrete and Manzur 2008). In light of the above, the aim of this study was 1) to determine the prey preference of *J. lalandii* and *M. africana* when exposed simultaneously to native (*A. atra, C. meridionalis*) and invasive (*M. galloprovincialis, S. algosus*) mussel prey and 2) to examine how these preferences might vary in a scenario where invasive prey species are most abundant. Based on research conducted prior to the invasions of *M. galloprovincialis* and *S. algosus* (Branch 1978; Griffiths and Seiderer 1980), it was predicted that both predators would select for the native mussel *C. meridionalis*, but when offered higher proportions of invasive mussels, both predators would select for the more abundant invasive species.

2.2 Methodology

For logistical reasons, these experiments had to be performed before the completion of the subtidal mussel surveys in Chapter 1. As such, at the time of designing this study the subtidal scarcity of *Mytilus galloprovincialis* was not yet known and thus this species was included in this chapter.

Specimen collection and maintenance

The four mussel species used in this study were collected from monospecific mussel beds to ensure accurate species identification. *Aulacomya atra* and *Mytilus galloprovincialis*

were collected from Bloubergstrand, *Choromytilus meridionalis* from Muizenberg, and *Semimytilus algosus* from Hout Bay (Fig. 2.1). The length of mussels used in experiments ranged between 20 – 30 mm. Rock lobsters and starfish were collected from the south coast at Kalk Bay Harbour and False Bay Yacht Club, respectively. As *S. algosus* had only recently (ca. 2015) spread to this section of the coast, and the current chapter was completed in 2015-2016, these sites were selected to ensure that native predators would not have been exposed to this species for a substantial period, if at all. Rock lobsters with carapace lengths between 65 – 75 mm and starfish with arm lengths within the range of 50 – 80 mm were used in experimental trials. These sizes were chosen based on previous research that demonstrated that individuals of these sizes feed on mussel prey with lengths of 20 – 30 mm (Griffiths and Seiderer 1980; Penney and Griffiths 1984).

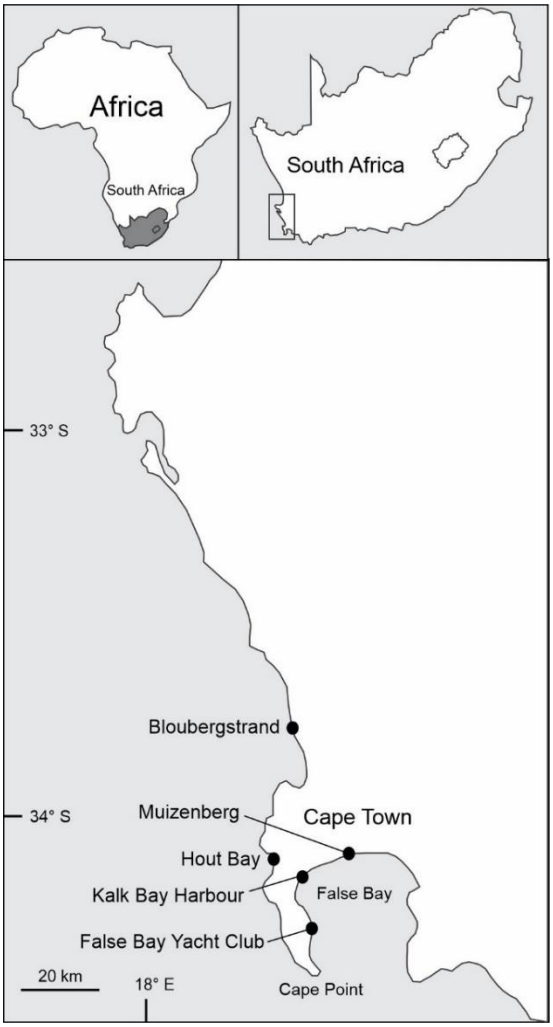

Figure 2.1: Collection sites of species along the west and south coasts of South Africa, separated by the biogeographic break at Cape Point. Bloubergstand - *Aulacomya atra, Mytilus galloprovincialis*; Muizenberg – *Choromytilus meridionalis, Semimytilus algosus*; Kalk Bay Harbour – *Jasus lalandii*; False Bay Yacht Club – *Marthasterias africana*.

Upon collection, all specimens were returned to the laboratory at Stellenbosch University and maintained in holding tanks with aerated artificial seawater at a salinity of 30 –

35 ppt. and at a constant temperature of 15°C. Water changes were carried out daily for rock lobsters and starfish, and twice daily for mussels. Mussels were supplied with algal culture every two days. In order to standardize hunger levels across all replicates, rock lobsters and starfish were starved for a period of seven days prior to experiments. However, during trials starfish took longer to commence feeding (ca. 20 days), which could be an indication that they require longer acclimatization or starvation periods, potentially as a result of their comparatively slower feeding rates (Penney and Griffiths 1984).

Feeding trials

Experiments were conducted separately for rock lobsters and starfish. Lobster experiments took place in tanks with bases measuring 40 x 70 cm and filled with 11 L seawater, whereas starfish trials took place in circular tanks of 23 cm diameter filled with 5 L seawater. Individual rock lobsters and starfish were offered one of three diet treatments that contained mussel species, scattered haphazardly in the tanks, in varying proportions representative of different invasion scenarios (Table 2.1). To account for potential differences driven by the sex of lobsters (Mayfield et al. 2000a) every diet treatment was replicated nine times each for males and females, with the exception of the 'Baseline' diet where logistical constraints resulted in only eight replicates for males. Due to lobsters being sensitive to visual cues (Hirtle and Mann 1978) experiments were monitored only once daily in order to avoid possible disturbances that could interfere with normal feeding behaviour. Lobsters that moulted during the acclimatization period or during trials were not used in experiments. Experiments with lobsters were run for a total of 10 days. Experiments with starfish consisted of 9 replicates of each of the three diets (Table 2.1). Due to their comparatively slower feeding rate (Penney and Griffiths 1984), these trials ran for a total of 40 days.

Table 2.1: Diet treatments consisting of native (*Aulacomya atra, Choromytilus meridionalis*) and invasive (*Mytilus galloprovincialis, Semimytilus algosus*) mussels that were offered to *Jasus lalandii* and *Marthasterias africana*. 'Pre-invasion' and 'Post-invasion' diet reflected the more recent invasion of the mussel *Semimytilus algosus*.

	Mussel composition			
Diet treatment	*A. atra*	*C. meridionalis*	*M. galloprovincialis*	*S. algosus*
Baseline	6	6	6	6
Pre-invasion	6	6	12	0
Post-invasion	3	3	9	9

Monitoring of experiments for both test species consisted of the identification, removal and replacement of consumed mussels, in order to maintain constant proportions of the respective diets throughout experiments. Controls for experiments with both predators were three replicates of each diet containing mussels but no predators, in order to confirm that

mussel mortality in the experimental tubs was attributable to predation and not due to other confounding factors.

Chesson selectivity index

A Chesson selectivity index was used in order to assess the prey preference of *Jasus lalandii* and *Marthasterias africana* towards the mussel species across the three diets (Chesson 1978). Selection toward particular species of prey was determined through the equation:

$$\alpha_i = \frac{(r_i/p_i)}{\Sigma_i(r_i/p_i)} \; ; \; i = 1, \ldots, n$$

where r_i is the percentage of a particular species in diet (consumed), p_i the percentage of that same particular species in the overall habitat (on offer) and n the total number of mussel species in the overall habitat (on offer). When $\alpha = 1/n$ neutral selection/the absence of selective predation in rock lobsters is indicated, whereas $\alpha < 1/n$ will infer negative selection (avoidance) and $\alpha > 1/n$ infers positive selection (preference). The use of this particular selectivity index is justified as it takes into account the presence of other prey items, thus incorporating the presence of multiple species (and in varying proportions) that are present in the overall habitat of the predator.

Assessments of prey preference indices for both rock lobsters and starfish were undertaken with repeated measures ANOVAs. For lobsters, ‘diet’ and ‘sex’ were employed as between factors, and index for each mussel species as a within factor. For starfish, ‘diet’ was designated a between factor and index for each mussel species as a within factor. Data were arcsine transformed prior to statistical analyses. Analysis was carried out in SPSS (Version 24.0, IBM 2016).

Mussel morphology and energetic content

To investigate some of the underlying factors that may drive foraging decisions made by rock lobster and starfish predators, several prey characteristics were assessed. These included among species differences in (1) shell strength that can mechanically limit the ability of lobsters to crush mussels (Juanes 1992), (2) adductor muscle size that may influence opening of mussels by starfish (Reimer and Harms-Ringdahl 2001) and (3) energetic content that may make particular species more sought after by predators (Creswell and McLay 1990). Ten individuals of each mussel species from the size class utilised during the feeding experiments were used to compare morphometric characteristics and energetic content. These mussels were collected from the same sites as those used in feeding trials (Fig. 2.1).

Shell strength was measured using a Zwick 1484 universal tensile tester and pressure was applied at a rate of 2 $mm.s^{-1}$. Shells were separated and the point of fracture was established for both valves, the average of which was used as a representation of individual mussel shell strength (Mackenzie et al. 2014). All shells were orientated in the same way during testing i.e. the shell length along the horizontal axis of the instrument with the outer shell facing upwards. The size of adductor muscles was determined by weight (Reimer and Tedengren 1997). After collection, posterior adductor muscles were separated from the rest of the flesh and dried to a constant weight at 60 °C, after which they weighed to the nearest 0.01 mg. Energetic content (kJ/g) was determined by removing the flesh from mussels and drying samples to a constant mass at 60 °C. Samples were then ground into powder form and the energy content was determined by bomb calorimetry. After meeting assumptions of normality and equal variances (determined through normal pp-plot and Levene's test, respectively), both morphometric characteristics and energy content were compared among mussel species using a one-way ANOVA followed by Tukey's HSD test.

2.3 Results

Mussel mortality as a result of predation by rock lobsters and starfish was confirmed through survival of all mussels in the control treatments.

Rock lobsters

No significant differences between male and female lobsters were detected in the 'Baseline' diet ($F_{3, 45}$ = 3, 45, p = 0.061), 'Pre-invasion' diet ($F_{2, 32}$ = 1.424, p = 0.256), or the 'Post-invasion' diet ($F_{3, 48}$ = 0.288, p = 0.834). Repeated measures ANOVA considering the Chesson selectivity indices for all respective mussel species revealed that there was a significant main effect of mussel species ($F_{3, 150}$ = 16.574, p < 0.001, Fig. 2.2a). This was driven by stronger selection for the native mussel *Choromytilus meridionalis* as revealed through post-hoc pairwise comparisons, where Chesson selectivity indices for *C. meridionalis* compared to other species were significantly different (p < 0.001) in all cases. There was no significant effect of 'diet' ($F_{2, 50}$ = 1.969, p = 0.15), and the 'diet' x 'prey' interaction was also non-significant ($F_{6,150}$ = 1.005, p=0.42). Notably, rock lobsters consumed all the flesh of mussels that they opened, suggesting that acceptance or rejection of prey was decided before consumption began.

Starfish

Repeated measures ANOVAs of the Chesson indices revealed a significant main effect of prey species ($F_{3, 15}$= 11.323, p<0.001, Fig. 2.2b). Post-hoc pairwise comparisons revealed this was driven by a significantly greater selection of the native mussel *C. meridionalis*

compared to the remaining mussel species ($p < 0.001$). Similarly to lobsters, starfish fully consumed all mussels that they opened.

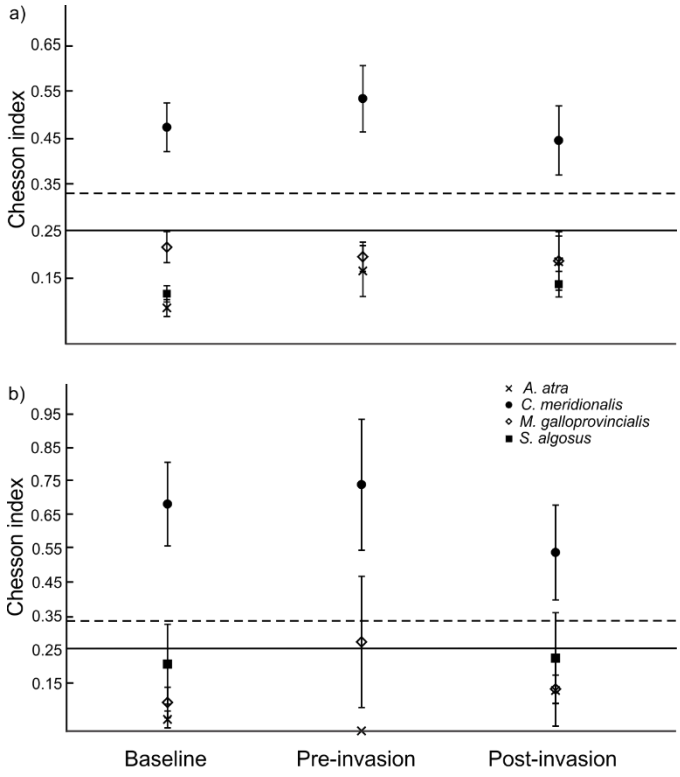

Figure 2.2: Chesson selectivity indices (mean ±SE) for native (*Aulacomya atra*, *Choromytilus meridionalis*) and invasive (*Mytilus galloprovincialis, Semimytilus algosus*) mussels as offered in the three 'diet' treatments to (a) rock lobsters *Jasus lalandii* (males and females grouped) and (b) starfish *Marthasterias africana*. For 'Baseline' and 'Post-invasion' diet, values above solid line = positive selection. For 'Pre-invasion' diet, values above dashed line = positive selection. Values below lines are indicative of avoidance and values on lines of neutral selection.

Mussel morphology and energetic content

Shell strength was found to vary among mussel species ($F_3 = 179.580$, $p < 0.001$) with the native mussel *A. atra* having the strongest shells (Fig. 2.3a). No difference in shell strength was found between *Mytilus galloprovincialis* and *C. meridionalis*, while the emerging alien *Semimytilus algosus* had the weakest shells. The size of adductor muscles also varied among species ($F_3 = 121.465$, $p < 0.001$) and was driven by *A. atra* having significantly larger muscles than all other species (Fig. 2.3b). The energy offered by the four mussel species differed significantly $F_3 = 13.92$, $p < 0.001$). Notably, the mean energy content of *S. algosus* individuals (10.5 kJ ± 0.3 SE) was significantly greater than of both native species *A. atra* (8.8 kJ ± 0.5)

and *C. meridionalis* (6.6 kJ ± 0.38; Fig. 2.3c). The preferred *C. meridionalis* had the lowest energy, differing significantly from all species except *M. galloprovincialis* (Fig. 2.3c).

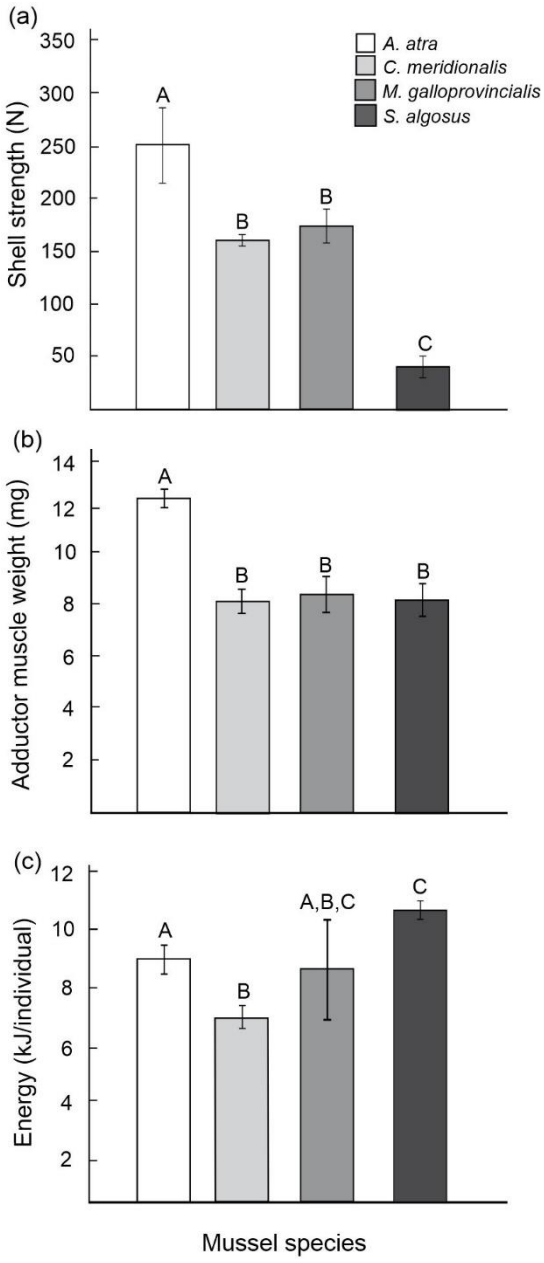

Figure 2.3: Mean (±SD) a) shell strength, b) adductor muscle weight, c) energetic content (± SE) of native (*Aulacomya atra, Choromytilus meridionalis*) and invasive (*Mytilus galloprovincialis, Semimytilus algosus*) mussels. Bars not sharing common letters are significantly different (Tukey's HSD test, $p < 0.05$).

2.4 Discussion

Invasions by alien prey species often result in strong competition with native counterparts (Crooks 2002; Shinen et al. 2009) and can lead to notable changes in the availability of native prey as a source of food for native predators (Carlsson et al. 2009). Novel invasive prey species can therefore come to represent an abundant food source for native

predators if they are able to switch towards feeding on invasive prey (Barber et al. 2008). However, there is also the possibility that predators may avoid novel invasive prey due to unfamiliarity, and may continue to select and consume native species, despite a potentially greater availability of the novel resource (Carlsson et al. 2009; Robinson et al. 2015). This study investigated this phenomenon with regards to two native subtidal predators, the rock lobster *Jasus lalandii* and starfish *Marthasterias africana*, and their selection preferences towards native and invasive mussel prey. Both of these predators demonstrated significant selection preferences toward the same native mussel, *Choromytilus meridionalis* above all other mussel species, even in diet treatments with higher proportions of invasive mussels *Mytilus galloprovincialis* and *Semimytilus algosus*. These results suggest avoidance of novel prey in both of these important predators, despite them being generalist predators that have been suggested to easily incorporate novel prey into their diets (Rodriquez et al. 2006; Carlsson et al. 2009).

Although there are studies that demonstrate native intertidal predators, such as the African Black Oystercatcher *Haematopus moquini* and the whelk *Trochia cingulata*, consume the established invader *M. galloprovincialis* (Coleman and Hockey 2008; Alexander et al. 2015a), only one study to date records the consumption of *S. algosus* by a native predator (the whelk *T. cingulata*) (Alexander et al. 2015a). Notably, the feeding behaviours of subtidal native predators and their responses to either of the invasive mussel species have until now remained unknown. Considering that *S. algosus* has a wide subtidal distribution which includes a recent expansion into False Bay (Chapter 1), the observation that both subtidal predators studied here avoided this novel prey is noteworthy. While the avoidance of *S. algosus* by native predators could most easily be explained by naivety, the avoidance of *M. galloprovincialis* was surprising given the long time period this invasive mussel has been present on the South African coastline (Grant and Cherry 1985). However, as Chapter 1 found *M. galloprovincialis* to be virtually absent from subtidal habitats, subtidal predators may in fact not have encountered it and may consequently be unfamiliar with feeding on this prey.

Nonetheless, to confirm that avoidance of the invasive mussels by lobsters and starfish was in fact the result of naivety, it is important to consider other factors that may affect prey choice by predators. A primary driver of prey choice is the ability of predators to handle prey and effectively access the energetic reward they offer (Hughes and Dunkin 1984a). In this study, comparisons of shell strength revealed that the invasive mussels *M. galloprovincialis* and *S. algosus* do not have stronger shells than the native mussel species. In fact, *S. algosus* had the weakest shells of all four species but was still not selected for by lobsters, despite them crushing mussel shells to access their prey. Starfish utilize a different approach to handling prey and pry open mussel prey. However, the avoidance of the invasive mussels by this predator could not be explained by adductor muscle strength as the invasive mussels did

not have larger adductor muscles than the native mussels. It is interesting to note that the avoidance of the native *Aulacomya atra* by lobsters is likely reflective of its strong ribbed shell. Previous comparative studies of the native mussels *A. atra* and *C. meridionalis* have illustrated that a larger force is required by rock lobsters to crush and detach *A. atra* than *C. meridionalis* of equal lengths (Griffiths and Seiderer 1980), and this coupled with unfamiliarity towards the invasive mussels, is a potential mechanism behind the preference toward *C. meridionalis*. Similarly, the selection for *C. meridionalis* by starfish likely relates to the larger adductor muscles of *A. atra* which together with unfamiliarity towards *M. galloprovincialis* and *S. algosus* drives the choice for *C. meridionalis*.

A primary driver of prey choice is the ability of predators to handle prey and effectively access the energetic reward they offer (Hughes and Dunkin 1984a). In this case, *C. meridionalis* in fact offers the lowest reward in terms of energetic content, a finding that aligns with a previous intertidal study that compared *C. meridionalis*, *A. atra*, and *M. galloprovincialis* (van Erkom Schurink and Griffiths 1991). This suggests that energetic content did not govern the selection of prey by these predators. It was also notable that acceptance or rejection of prey took place before mussels were opened. This, together with findings on shell strength, adductor muscle size, and energetic content, suggests that prey choice by these predators may reflect one of two scenarios: 1) unfamiliarity with the invasive mussels, or 2) prey choice may not be governed by the traditional optimal foraging theory framework that assumes prey is selected to maximize energetic gain. Recent research suggests that some predators might not forage to optimize net energetic gain, but rather manage the intake and balance of macronutrients (Machovsky-Capuska et al. 2016). Various fitness-related aspects (e.g. egg production (Jensen et al. 2012), longevity (Lee et al. 2008), immunity (Le Couteur et al. 2015)) have been suggested to be linked to the ability of predators to actively select for particular nutrients while foraging. To determine whether the predators studied here are foraging in this way, additional studies that consider the nutritional composition of different prey species would be required. However, it is unlikely that taxonomically different organisms such as rock lobsters and starfish have the same nutritional requirements, given the large differences in their physiology and life-histories. As such, the selection and avoidance of similar prey species by both predators is probably explained by the unfamiliarity of avoided prey rather than by prey nutritional composition.

Positive selection towards *C. meridionalis* occurred across all diet treatments, even when proportions of other species were greater. This was an unexpected finding given the generalist nature of the predators in the study (Barkai and Branch 1988a,b; Edgar 1990; Mayfield et al. 2000a; Mayfield and Branch 2000) and discounted the second hypothesis (i.e. that prey selection would shift toward invasive species when they were more abundant than *C. meridionalis*). It has been suggested that generalist predators, such as rock lobsters and

starfish, switch to alternative prey as the density of their main prey declines. According to the alternative prey hypothesis (Angelstam et al. 1984), the predation pressure on such alternative prey (e.g. *A. atra*, *M. galloprovincialis* and/or *S. algosus* in this case) should increase as the density of the main prey (i.e. *C. meridionalis*) decreases (Pöysä et al. 2016). The results of this study demonstrate, however, that both predators continue to select *C. meridionalis* even when it is the least abundant prey species. If this was to occur in the field, then predation on *C. meridionalis* by rock lobsters and starfish may in fact facilitate continued invasion of *S. algosus*. Continued predation on *C. meridionalis* could increase availability of primary rock space (Needles et al. 2015), a crucial resource of sessile organisms (Stachowicz et al. 2002; Branch et al. 2008). This is not the first observation of native predators failing to select for invasive prey (e.g. López et al. 2010; Veiga et al. 2011), although in these cases avoidance was suggested to be reflective of predators facing mechanical constraints to foraging on the novel prey. In contrast, this study found that alien prey were unlikely to offer predators such constraints. This chapter demonstrated that two important native predators, the rock lobster *J. lalandii* and starfish *M. africana*, select for native over invasive mussel prey species despite the fact that they were offered in reduced proportions. As generalist predators, these results were unexpected. In the broader context, these findings highlight that predator-driven biotic resistance may not manifest, even in the context of generalist predators. Importantly, when such avoidance coincides with selection of native prey that may have offered invasion resistance through inter-specific competition, these predators may indirectly facilitate invasions. While it is presently unclear how often such facilitation acts, interrogating the behaviours that drive such outcomes will advance our understanding of successful invasions.

CHAPTER 3:

Avoidance of *Semimytilus algosus* by *Jasus lalandii* breaks down as a result of multiple predator effects

Abstract

Most natural communities contain multiple predators that utilize shared prey resources. The presence of multiple predators can lead to variation in predator behaviour, such as alterations in prey preference. This, in turn, may result in increased or decreased predation risk for the shared prey. While this concept is well-established in community ecology, it has not been extensively accounted for in studies that consider predator-driven biotic resistance from native predators against invasive prey. Whelks (*Burnupena* spp.) and rock lobsters (*Jasus lalandii*) are subtidal native predators that can co-occur along the South African west and south coasts, with both predators known to consume mussels. This chapter determined the prey preference of these predators in isolation and when co-occurring, with the aim to assess multiple predator effects (MPEs) within this system and the implications of this for invasive mussel prey. Prey preference was established for each predator when exposed to varying relative proportions of three mussel species (native *Aulacomya atra* and *Choromytilus meridionalis*, and invasive *Semimytilus algosus*), with the relative proportions representative of current and future invasion scenarios. To examine MPEs for each prey species, a multiplicative risk model was used to generate values for predicted proportions of prey consumed, that were then compared to observed proportions. Both predators exhibited a preference toward the native *C. meridionalis* when they occurred alone, but prey selection become more varied for lobsters when co-occurring with whelks. All prey species experienced significant MPEs when predators co-occurred, which resulted in increased risk for prey in all invasion scenarios. Overall, combined predation pressure was strongest on *C. meridionalis* and invasive *S. algosus*. Importantly, these results indicate that the combined predatory efforts from two co-occurring native predators can result in stronger predation pressure on invasive prey than would have been recognised if predators had been assessed in isolation. In this case it resulted in stronger predation pressure on the invasive *S. algosus* and suggests increased potential for biotic resistance against this prey.

3.1 Introduction

There are various factors that can influence the foraging decisions made by native predators, which may hold important implications for the realization of predator-driven biotic resistance against alien prey. The presence of co-occurring predators utilizing the same prey resources may result in strong competition when these resources are limited (Osenberg 1989).

Classic ecological theory predicts that the strength of any resulting competitive interactions will increase as more species occupy the same niche and/or when resources become limited (Pianka 1974). Consequently, inferior competitors can be pressured to select for alternative, perhaps sub-optimal resources or, in extreme cases, be excluded from a community (Fernandez et al. 2017; Sánchez-Hernández et al. 2017; Klompmaker and Finnigan 2018). It is well-established that most natural communities contain multiple predators (Sih et al. 1998; Navarrete et al. 2000; Van Son and Thiel 2006) and their co-occurrence can have a variety of direct and indirect effects on their prey (Siddon and Witman 2004) and thus community composition (Navarrete et al. 2000). While direct effects of predators are easily determined (e.g. either a prey is eaten or not), indirect effects can be complicated to examine but nonetheless account for significant variation in interaction outcomes and community composition (Morgan et al. 2016).

Indirect effects can manifest via two mechanisms: density-mediated indirect interactions (DMIIs) and trait-mediated indirect interactions (TMIIs) (Werner and Peacor 2003). Classic examples of DMIIs are trophic cascades, whereby the density of a predator population affects the density of their prey's population, which in turn affects other species that also interact with the prey (Menge 1995; Mayfield and Branch 2000; O'Connor et al. 2013). TMIIs, also referred to as behavioural indirect interactions (Abrams 1995), are behavioural changes of one species in the presence of another, that can indirectly affect the abundance of a third species (Werner and Peacor 2003; Siddon and Witman 2004). For example: when alone, predator A selects for prey A. However, in the presence of predator B, predator A modifies its foraging behaviour which can result in a different net predatory impact on prey (Sih et al. 1998; Navarrete et al. 2000). This can result in multiple predator effects (MPEs) on prey, which can be defined as the effect(s) of multiple predators on prey that cannot be predicted by simply summing the effects of each predator species in isolation (Sih et al. 1998). A study by Siddon and Witman (2004) of a rocky subtidal community illustrated MPEs of crab and lobster predators on their shared prey i.e. sea urchins. It was found that when crabs were the only predators present, urchins were their main prey. However, when lobsters were added to the community, crab predation on the urchins decreased, even though the lobsters did not display strong preference toward urchins. The strength of the crab-urchin interaction further decreased when an alternative prey was added to the local prey base (Siddon and Witman 2004). Similarly, Gaymer et al. (2001) found that two predatory starfish species preferred prey of the same species and size when in isolation. When they co-occurred, however, prey selection become more variable and alternative prey were incorporated into their diets. This has been suggested as a mechanism whereby competition between the two predators is minimized (Gaymer et al. 2001).

Indirect effects of multiple predators on prey may have important implications for alien prey invasions and the potential for predator-driven biotic resistance against such prey. The majority of studies examining predator-driven biotic resistance focus on direct effects of native predators on alien prey. This leaves a substantial research gap regarding the possible changes in consumption rates and/or prey selection of multiple, co-occurring native predators and the potential consequences for alien prey. Such studies may provide valuable insight into the potential for biotic resistance at a community level.

In subtidal habitats on the South African west coast, rock lobsters (*Jasus lalandii*) and whelks (*Burnupena* spp.) are co-occurring predators that share a common prey in the form of mussels. Moreover, previous research has demonstrated that when at high densities, *Burnupena* whelks can predate on *J. lalandii* at extremely high rates, to the extent that lobsters can be completely excluded from the community (Barkai and Branch 1988a; Barkai and McQuaid 1988). When these whelks occur at lower densities, however, they can be readily predated upon by *J. lalandii*. Such predator-prey role reversals can have large impacts on community composition. Indeed, communities dominated by *J. lalandii* differ significantly from those dominated by *Burnupena* (Barkai and Branch 1988b). In Chapter 2, it was revealed that *J. lalandii* exhibits strong selection toward the native mussel, *Choromytilus meridionalis*, while avoiding the invasive mussels *Semimytilus algosus* and *Mytilus galloprovincialis*. The prey preference of *Burnupena* when exposed to mussel communities such as those described in Chapters 1 and 2 is not yet known. It is also unknown if the co-occurrence of rock lobsters and whelks may impact their respective foraging decisions and the ultimate predation pressure experienced by their shared prey. The aims of this study were to assess whether prey selection by the two predators will change when they co-occur and, if so, to consider the implications thereof for the consumption of the invasive mussel *S. algosus*.

Based on the results of Chapter 2, it was predicted that *J. lalandii* would select for the native *C. meridionalis*, regardless of the presence or absence of whelks. In the absence of previous studies considering feeding by *Burnupena* whelks, it was predicted that whelks would exhibit random prey selection in isolated- and multiple predator experiments. As such, it was hypothesized that regardless of the presence of multiple predators, predation pressure would be focussed on the native *C. meridionalis*, with lobsters and whelks offering little predator-driven biotic resistance to the invasion by *S. algosus*.

3.2 Methodology

Specimen collection and diet treatments

Mussels for all experiments were collected from the same sites described in Chapter 2 and had shell lengths 20 – 30 mm. All rock lobsters and whelks were collected from Sea Point on the Atlantic Seaboard of the Cape Peninsula (33º55’13’’S, 18º22’48’’E). No discrimination

was made between male and female rock lobsters as Chapter 2 found no difference in prey selection between the sexes. It is important to note that both predators used in this study occur at all sites where mussels were collected, thereby accounting for the potential impacts of predator cues on the morphological development of mussels (Caro and Castilla 2004; Sherker et al. 2017).

Predators were offered one of two diet treatments each containing the three prey species but in different relative proportions. These treatments will be referred to hereon as a current diet or a future diet. The current diet is based on the current proportions at which the three mussel species occur subtidally, as reported in Chapter 1. These communities consist of the native *Aulacomya atra* in highest abundance, followed by smaller but fairly equal proportions of native *Choromytilus meridionalis* and *Semimytilus algosus* (hence the ratios for the current diet = 2 *A. atra* : 1 *C. meridionalis* : 1 *S. algosus*). The future diet mimics a scenario where the invasive *S. algosus* becomes the dominant subtidal mussel species and is based on the invasion success of this species in intertidal (de Greef et al. 2013; Sadchatheeswaran et al. 2015; Zeeman et al. 2018) and subtidal (Chapter 1) environments. As such, the ratios for the future diet were 1 *A. atra* : 1 *C. meridionalis* : 2 *S. algosus*).

Determining prey selection of isolated predators

The prey preference of rock lobsters and whelks when foraging in isolation was determined in the laboratory. This was due to safety- and security-related challenges of performing field experiments in the study region. Animals were kept in aerated seawater at 13^0C, which is reflective of field water temperatures along this section of the South African coast. During experiments, mussels were placed randomly within each experimental tank. Experimental tanks were checked daily, and consumed mussels were identified, counted, and replaced in order to maintain constant proportions of prey species throughout the experiments. Survival of mussels in holding tanks was monitored to verify that mussel mortality in experimental tanks was due to predation and no other factors.

Experiments with whelks were performed in 11l experimental tanks with a base of 0.5 m^2. Water changes were carried out every three to four days. For whelk experiments each experimental tank contained 50 randomly selected whelks with an average shell length of 31.9 (±4.9 SD) mm. This density was chosen to reflect field densities of 100 whelks/m^2 in Sea Point where the whelks were collected. Whelk experiments were conducted using groups of whelks rather than individuals because preliminary field observations revealed that they feed cooperatively. Whelks were starved for seven days after collection to standardise hunger levels. This was followed by a 25-day feeding experiment to establish prey preference. Each diet (current, future) was replicated 10 times. Whelks were offered a total of 12 mussels,

constituted of the different ratios among the species depending on the diet under consideration.

Although the prey preference of *Jasus lalandii* was examined in Chapter 2, it required re-assessment as *M. galloprovincialis* (a prey species included in Chapter 2) had since been found to be absent from subtidal habitats (Chapter 1). Experiments with rock lobsters (carapace length 70 – 120 mm) were undertaken in 38l experimental tanks with one lobster per tank. A seven-day starvation and acclimation period was implemented prior to experiments. For each diet (current, future) 10 replicates were considered, and the experiment was performed over a period of seven days as the high feeding rate of lobsters generated data much faster than was recorded for whelks. This high feeding rate also required that lobsters were offered double the number of mussels offered to whelks. In the absence of these high numbers, all mussels were consumed and prey preference could not be assessed.

Determining prey selection of co-occurring predators

A natural, sheltered 575 m^2 rock pool located in Sea Point was chosen to examine the prey selection of co-occurring rock lobsters and whelks. This was done to ensure that prey selection was determined with both predators at ecologically relevant densities, a requirement that could not be met in the laboratory due to logistical constraints associated with the large tanks required. The rock pool had a rocky substratum and naturally supported *Burnupena* whelks. In addition to whelks, other naturally occurring macrofauna included winkles (*Oxystele sinensis*), cushion stars (*Parvulastra exigua*), brittle stars *(Ophioderma wahlbergii*) and green algae (*Ulva fasciata*). The pool also supported *Burnupena* whelks with a mean density of 102 (± 27 SE) whelks/m^2. This density was quantified by counting the number of whelks in 30 randomly placed replicates measuring 0.25 m^2. As such the whelk densities applied in the laboratory (100 whelks/m^2) were maintained during the field experiment. Similarly, whelks used in the laboratory and field experiments did not differ in size (laboratory whelks: 31.9 ± 4.9 mm SD; field whelks: 29.1 ± 6.3 mm). No mussels were present in the pool. This was an important consideration as it avoided prior conditioning of whelks toward any particular mussel species, and so that no other mussels were available to predators during the experiment. A large population of rock lobsters was present on the seaward side of the pool, resulting in an easy introduction to the rock pool and thereby offering a good setting to experimentally test prey preference of the two predators when co-occurring.

Seven days prior to the experiment, 131 *J. lalandii* (71 large (carapace length > 100 mm); 60 small (carapace length <100 mm)) were collected and maintained in the Marine Research Aquarium of the Department of Agriculture, Forestry and Fisheries in Sea Point. After a seven-day starvation period the lobsters were released into the rock pool. This achieved

a density of rock lobsters (0.22/m^2), closely resembling current densities (Mayfield and Branch 2000; Mead et al. 2013).

Submersible steel frames were used to offer predators mussels during the field experiment (Fig. 3.1). Mussels were randomly placed onto Perspex plates (20 x 20 cm) and secured using Bostik Marine Silicon Sealant, a non-toxic product developed explicitly for use in marine aquaria. The Perspex plates were then secured onto multiple steel frames (Fig 3.1). The relative positions of the different diet plates were randomised for each steel frame, with the plates on each structure separated by at least 0.5 m. Eight replicate plates were offered of each diet treatment.

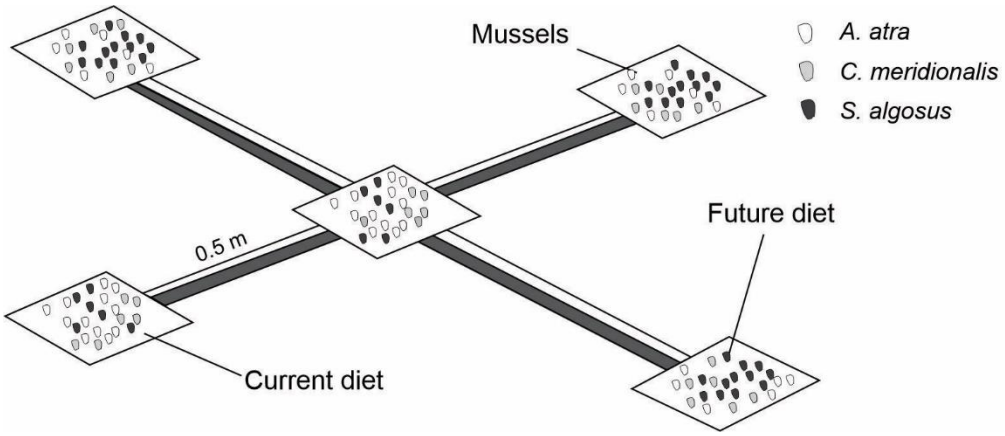

Figure 3.1: Submersible steel frame with attachment points for mussel plates with mussel species in proportions representative of the current or future diet treatments. Different coloured mussel shapes represent the three prey species (*Aulacomya atra, Choromytilus meridionalis*, *Semimytilus algosus*).

Rock lobsters were released into the rock pool two hours prior to the start of the experiment to allow time for acclimation. The steel frames with mussel plates attached were subsequently placed into the pool and left overnight for 12 hours (18:00 – 06:00). This timing was chosen as both predators preferentially feed at night. Placement of the frames was done randomly and at least 3 m away from each other. After the 12-hour experimental period the frames were returned to the surface. For each diet the number of mussels eaten per species was recorded. Additionally, the source of predation (whelk or lobster) was identified. This was done by drawing on observations made during laboratory trials that indicated that the valves of mussels eaten by whelks remained attached but gaping, with flesh removed. Notably these shells remained glued to the plates. In contrast, mussels eaten by lobsters were removed from the plates and, as such, mussels that were missing were designated as eaten by rock lobsters.

Multiple predator effects

Effects of multiple predators on prey can be determined through a comparison between the observed and the predicted proportion of prey consumed (Sih et al. 1998; Liu et al. 2017). In order to generate values for the predicted proportions of prey consumed and to account for additive effects of multiple predators on prey, a multiplicative risk model was used (Soluk and Collins 1988; Sih et al. 1998):

$$C_{ab} = N(P_a + P_b - P_aP_b)$$

where C_{ab} is the predicted proportion of prey consumed when predator *a* and predator *b* are foraging together, N is the number of prey offered to co-occurring predators, P_a is the proportion of prey consumed when predator a forages in isolation, and P_b is the proportion of prey consumed when predator b forages in isolation. The P_aP_b term accounts for the prey consumed by one predator that cannot consequently be consumed by the other predator. Values for P_a and P_b were derived from isolated laboratory experiments with whelks and rock lobsters. Observed proportions of prey consumed were calculated as the mean daily number of prey consumed per predator (whelk, rock lobster) per diet treatment (current, future). Using proportional data in this case is also useful as it accounts for the different timeframes of experiments with whelks and rock lobsters. To generate predicted values for the multiple predator treatment (i.e. when whelks and rock lobsters co-occur), replicate data from the two isolated predator experiments were paired in all possible combinations. The mean and SD of these data were calculated and represented the final predicted value of prey consumed for each prey species, in each diet treatment.

Statistical analyses

The prey preference of whelks and rock lobsters in isolation and co-occurrence experiments was determined through calculation of the Chesson index of selectivity (Chesson 1978) for each prey species (refer to Chapter 2 section 2.2 for a more detailed description of this index). All Chesson indices were arcsine transformed prior to analyses in order to be released from a proportional nature. For each predator, prey preference in isolation and co-occurrence experiments were analysed by comparing the Chesson indices for each prey species using mixed effects models and the 'lme4' package (Bates et al. 2015) in R (R Core Team 2015). The associated assumptions were met in all cases. For all analyses the saturated model included prey species (*A. atra, C. meridionalis, S. algosus*), diet treatment (current, future), and the interaction between these two variables as fixed factors. 'Experimental tank' was considered a random factor in isolation experiments, whereas 'plate number' was assigned this designation in the multiple predator experiment. The best fit model of each

experiment was selected based on Aikaike's Information Criterion (AIC), and Wald tests were used to determine the significance of the fixed factor(s) in each best fit model.

A multiple predator effect is confirmed when there is a significant difference between the predicted and observed proportion of prey consumed in a multiple predator environment (Sih et al. 1998; Liu et al. 2017). For each prey species, a two-way ANOVA was used to compare the predicted and observed proportions consumed in the two diet treatments. In addition, among species comparisons of the observed proportion consumed were undertaken to identify differences in predation risk when predators co-occur. This was done using a two-way ANOVA with prey (*A. atra, C. meridionalis, S. algosus*) and diet treatment (current, future) as fixed factors. Assumptions of normality and equal variances were met in all cases.

3.3 Results

Mortality of mussels due to predation by whelks and lobsters was confirmed through 99% survival mussels in the holding tanks that lacked predators.

Prey selection by whelks

When foraging alone, the best fit model explaining prey selection by *Burnupena* included prey species, diet and the interaction between these two factors (Fig. 3.2a, Table 3.1). However, only prey identity and the interaction between prey and diet significantly affected prey selection of whelks.

The non-significant effect of diet was likely driven by the consistently low Chesson index values of *Aulacomya atra* in both diet treatments. However, the significant interaction between diet and prey, likely driven by the lower Chesson index values of *Semimytilus algosus* in the future diet, suggests that diet could still have affected prey selection to some degree. The native *Choromytilus meridionalis* was consistently positively selected for by whelks while *A. atra* was actively avoided, regardless of diet treatment. Shells of consumed mussels lacked drill holes, suggesting that *Burnupena* do not drill through mussel shells to access the flesh. Instead, they insert their proboscis through gaping mussel valves, a method of feeding referred to as pedal handling (Gutiérrez and Gallardo 1999).

In the multiple predator experiment, the best fit model describing prey selection by *Burnupena* contained all three fixed factors (Fig. 3.2b, Table 3.1). However, the only significant main effect was prey species (Table 3.1). This is likely a reflection of the consistently very low Chesson index of *A. atra*. Notably, when co-occurring with lobsters, whelks actively selected for *C. meridionalis* and *S. algosus*, while *A. atra* was still avoided.

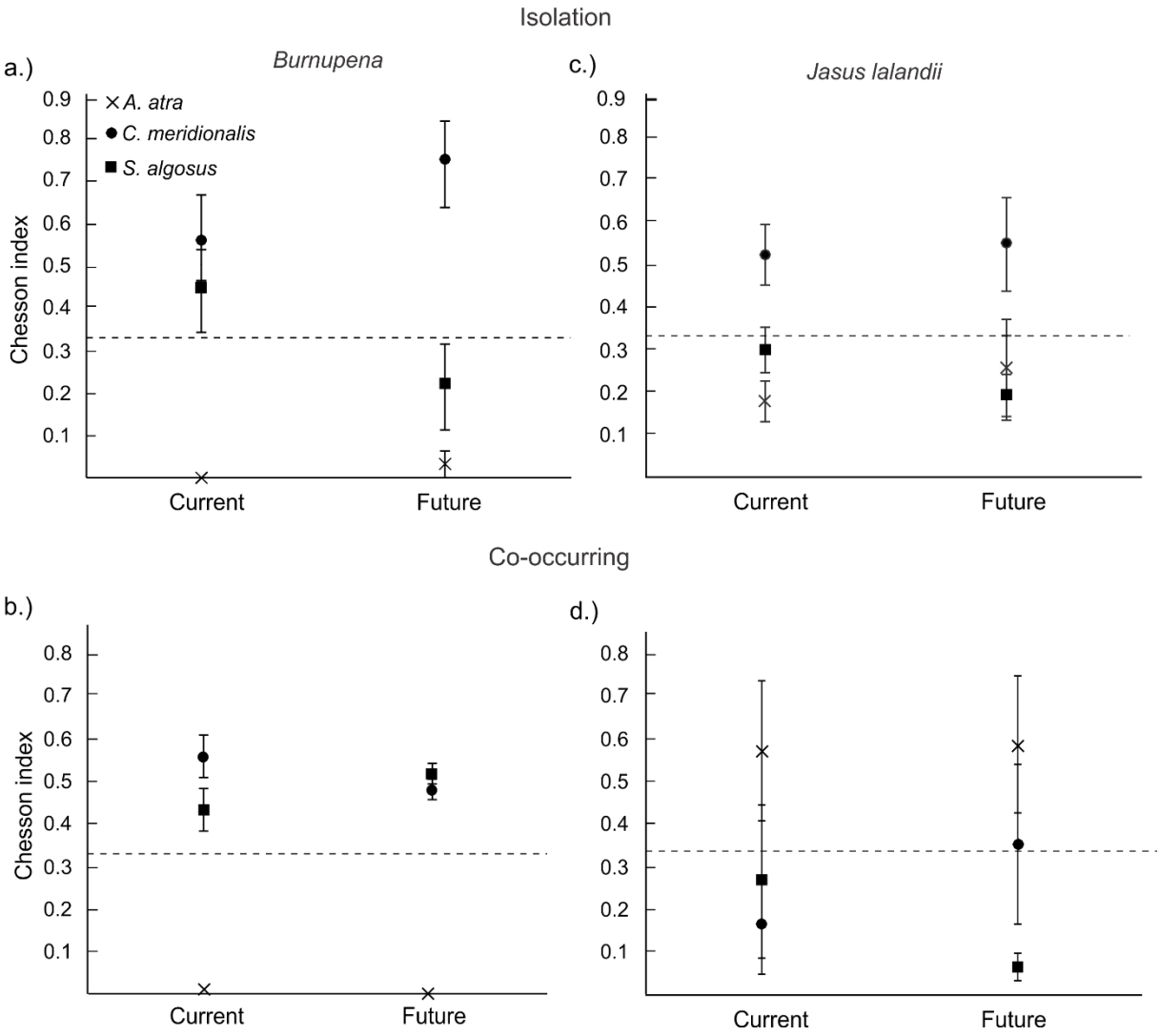

Figure 3.2: Chesson selectivity indices (mean ± SE) of three mussel species (native *Aulacomya atra, Choromytilus meridionalis* and invasive *Semimytilus algosus*) as presented to two predators, *Burnupena* whelks and *Jasus lalandii* in two diet treatments (current, future) when they forage in isolation (a, c) and when they co-occur (b, d). Values above the line = positive selection, values on the line = neutral selection and values below the line = active avoidance.

Table 3.1: Results of Wald tests examining the significance of the fixed factors in the best fit models of prey selection by *Burnupena* when foraging in isolation and when co-occurring with *Jasus lalandii*. This is followed by overall comparisons among coefficient estimates for three prey species (*Aulacomya atra, Choromytilus meridionalis*, *Semimytilus algosus*) as selected by *Burnupena*.

Isolated *Burnupena*			
Main effects	X^2	df	p
Prey	57.089	2	< 0.001
Diet	< 0.0001	1	1.000
Prey : Diet	7.986	2	0.018
Coefficient estimates for comparisons between prey species			
	C. meridionalis	*A. atra*	*S. algosus*
C. meridionalis	---		
A. atra	-0.522, p < 0.001	---	
S. algosus	-0.044, p = 0.701	0.478, p < 0.001	---
Burnupena co-occurring with *J. lalandii*			
Main effects	X^2	df	p
Prey	634.7887	2	< 0.001
Diet	0.0973	1	0.75512
Prey : Diet	5.8924	2	0.05254
Coefficient estimates for comparisons between prey species			
	C. meridionalis	*A. atra*	*S. algosus*
C. meridionalis	---		
A. atra	-0.813, p < 0.001	---	
S. algosus	-0.129, p = 0.009	0.684, p < 0.001	---

Prey selection by rock lobsters

When foraging alone, the best fit model explaining prey selection by *Jasus lalandii,* contained prey species and diet, but not the interaction between these two factors (Figure 3.2c, Table 3.2). Prey identity was the only factor that had a significant effect on prey selection by *J. lalandii*, with lobsters demonstrating positive selection towards *C. meridionalis* (Figure 3.2c). This was also reflected in the Chesson index values for *C. meridionalis* being significantly greater than that of the other two species (Table 3.2).

The foraging decisions made by rock lobsters when co-occurring with whelks differed from when they occurred alone. The best fit model contained all three predictors (prey species, diet, and the interaction between these factors), although once again only the effect of prey species was significant (Figure 3.2d, Table 3.2). When feeding in the presence of whelks, lobsters most often ate the native mussel *A. atra*, a species that they seldom fed on when feeding in isolation. Despite this clear trend and the identification of prey species as a significant main effect, coefficient estimates detected no significant pairwise differences among

the prey species. This lack of pairwise differences is likely driven by the elevated variability in prey selection by *J. lalandii* when feeding in the presence of whelks (Figure 3.2d).

Table 3.2: Results of Wald tests examining the significance of the fixed factors in the best fit models of prey selection by *Jasus lalandii* when foraging in isolation and when co-occurring with *Burnupena*. This is followed by overall comparisons among coefficient estimates for three prey species (*Aulacomya atra, Choromytilus meridionalis, Semimytilus algosus*) as selected by *J. lalandii.*

Isolated *J. lalandii*			
Main effects	X^2	df	p
Prey	12.243	2	0.002
Diet	0.073	1	0.787
Coefficient estimates for comparisons between prey species			
	C. meridionalis	*A. atra*	*S. algosus*
C. meridionalis	---		
A. atra	-0.410, p = 0.001	---	
S. algosus	-0.385, p = 0.003	0.026, p = 0.844	---
J. lalandii co-occurring with *Burnupena*			
Main effects	X^2	df	p
Prey	6.7072	2	0.035
Diet	0.0040	1	0.949
Prey : Diet	1.4119	2	0.494
Coefficient estimates for comparisons between prey species			
	C. meridionalis	*A. atra*	*S. algosus*
C. meridionalis	---		
A. atra	0.638, p = 0.231	---	
S. algosus	0.148, p = 0.633	-0.490, p = 0.113	---

Multiple predator effects

The expected and observed proportions of prey consumed differed significantly in cases with all three prey species (Fig. 3.3, Table 3.3). Importantly, post hoc pairwise comparisons revealed that for each prey species, the observed proportions consumed in the multiple predator environment was significantly larger than expected, confirming the existence of emergent multiple predator effects in this system.

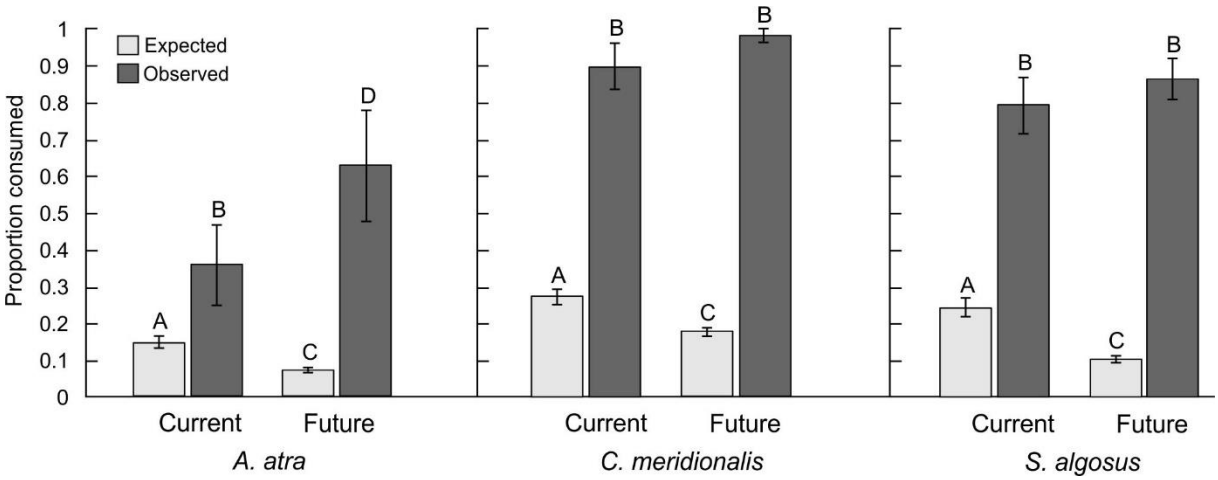

Figure 3.3: Comparisons of expected and observed proportions (mean ± SE) of mussel prey consumed (*A. atra, C. meridionalis, S. algosus*) in each diet treatment (current, future) in an environment where whelks and rock lobsters co-occur. Bars with different letters indicate significant differences (Tukey HSD, $p < 0.05$).

Table 3.3: Results of two-way ANOVAs comparing proportions of prey consumed between effects (expected, observed) and diet treatments (current, future).

	Effect	Diet	Effect*Diet
A. atra	$F_1 = 98.95$, $p < 0.001$	$F_1 = 3.417$, $p = 0.066$	$F_1 = 19.79$, $p < 0.001$
C. meridionalis	$F_1 = 383.97$, $p < 0.001$	$F_1 = 13.378$, $p < 0.001$	$F_1 = 6.028$, $p < 0.05$
S. algosus	$F_1 = 227.55$, $p < 0.001$	$F_1 = 21.6$, $p < 0.001$	$F_1 = 5.902$, $p < 0.05$

The observed proportions of consumed prey differed significantly among the three prey species ($F_2 = 13.801$, $p < 0.001$), but not between diet treatments ($F_1 = 3.829$, $p = 0.057$). Patterns of prey consumption in the two diet treatments were similar, resulting in a non-significant interaction between proportions of prey consumed and diet treatment ($F_2 = 0.788$, $p = 0.462$).

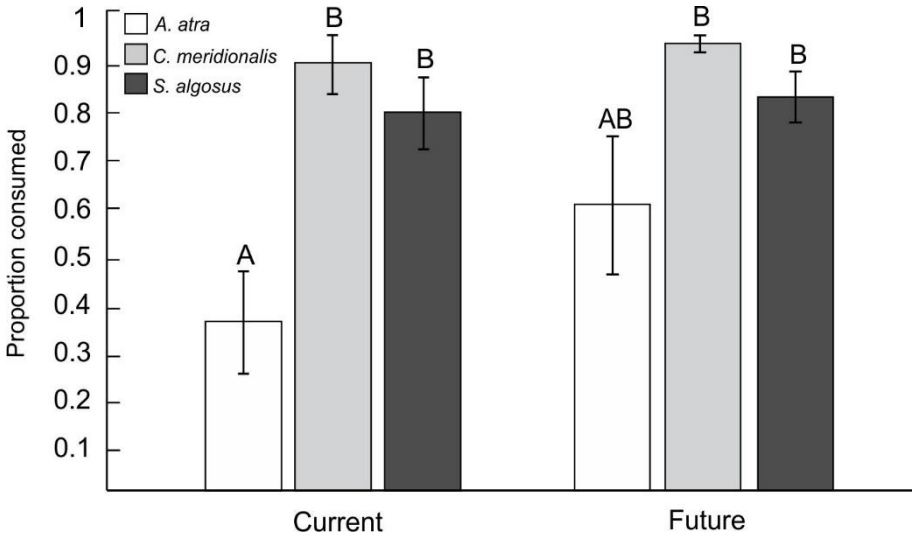

Figure 3.4: Observed proportions (mean ± SE) of prey (*A. atra, C. meridionalis, S. algosus*) consumed in the two diet treatments (current, future) in an environment containing whelk and rock lobster predators. Bars with different letters differ significantly (Tukey HSD, $p < 0.05$).

3.4 Discussion

When native predators fail to consume novel invasive prey and continue to consume native prey, it can reduce competition between trophically similar native and invasive prey and lead to indirect facilitation of alien prey invasions (Veiga et al. 2011). However, prey selection by native predators can be context dependent and can vary based on several factors, including the presence of other native predators that compete for the same food source. This chapter examined the feeding behaviour of two native predators, whelks (*Burnupena* spp.) and rock lobsters (*Jasus lalandii*) when they occur in isolation versus when they co-occur. Overall, whelks exhibited similar prey selection in isolation and in the presence of rock lobsters, while rock lobsters became more variable in the presence of whelks. In addition, significant multiple predator effects (MPEs) on mussel prey was detected for all species, regardless of how abundant the invasive mussel *Semimytilus algosus* was. Notably, even the native mussel *Aulacomya atra* that was almost ignored by predators foraging in isolation experienced increased predation risk when the two native predators co-occurred.

This study provides the first insights into prey selection of whelks of the genus *Burnupena* along the coast of South Africa. The results suggest that *Burnupena* actively selects for *Choromytilus meridionalis* and *S. algosus*, both when foraging alone and when co-occurring with another predator. In contrast to drilling whelks, *Burnupena* consume mussels through pedal handling, where whelks open mussels by inserting their proboscis between gaping mussel valves (Gutiérrez and Gallardo 1999). As such, it is unlikely that shell thickness plays a role in prey selection by *Burnupena*. Instead, it is possible that the strength of the

adductor muscles of mussel prey is more important in determining handling time and thus foraging decisions. The adductor muscle weight (used as a proxy for strength) of the three prey species used in this study is known to be greatest for *A. atra* (Chapter 2), with no difference between *C. meridionalis* and *S. algosus*. This likely explains the avoidance of *A. atra* by *Burnupena* in all experiments. Whelks in the future diet displayed negative selection of *S. algosus* in the isolated predator environment (laboratory), which changed to positive selection in the multiple predator environment (field). While the reason for this is currently unclear, one possibility is that whelks in the field had higher hunger levels than those in the laboratory. In the laboratory, whelks were starved for seven days prior to the experiment and they took longer to start feeding than anticipated. In the field, however, there was an overall scarcity of food which was noted approximately two weeks before the field experiment commenced. Furthermore, in the field experiment, whelks moved toward experimental plates shortly (within an hour) after deployment in the rock pool. It is suggested that whelks in the field might have had higher hunger levels than those in the laboratory and could thus have been less selective than those in the laboratory. This could also have contributed to the large discrepancy between expected and observed values of proportions of prey consumed in the multiple predator effects.

When *J. lalandii* foraged in isolation, it exhibited a strong preference toward *C. meridionalis*, regardless of the abundance of other prey species. This is in line with the findings of Chapter 2. When co-occurring with whelks, however, the prey selection of *J. lalandii* demonstrated a very different pattern. Under these conditions, prey selection became more variable with the native *A. atra* being eaten most often. There are various possible explanations for this discrepancy in prey selection by *J. lalandii* when foraging in isolation compared to when it co-occurs with *Burnupena*. Previous studies considering the interaction between these two predators have shown that *Burnupena*, when present in high densities, can represent a significant predatory threat to *J. lalandii* (Barkai and McQuaid 1988). In fact, when whelks are numerically dominant, they can exclude lobsters by mobbing and consuming them (Barkai and McQuaid 1988). Although the density at which point *Burnupena* switch from being lobster prey to lobster predators is not known, it appears that the density in this study (i.e. 100 whelks.m^{-2}) was sufficient to deter lobsters from their usual feeding patterns. It is possible that rock lobsters could have detected whelk cues and, after associating these with a potential threat, attempted to minimize interactions by feeding on mussels that were not being fed on by whelks. Indeed, the high densities in which whelks have been observed feeding on a single mussel (personal observation) could have prevented rock lobsters from attempting to attack certain mussels. Notably, the strength of competition between co-occurring predators is expected to be strong in communities with limited food availability (Abrams and Ginzburg 2000; Van Son and Thiel 2006). Competition for mussel prey in the multiple predator experiment was assumed to be strong as the rock pool is naturally devoid of mussels. As rock lobsters are generalist predators

(Mayfield et al. 2000a; Haley et al. 2011), it is possible that they might have switched to alternative prey to avoid competition with whelks. Unfortunately, logistical constraints prevented systematic direct observations and video footage of the multiple predator experiment, which would have been useful in elucidating potential predator-predator interactions occurring on or around the mussel plates.

Emergent multiple predator effects (MPEs) on shared prey result when the impacts on prey differ from what would have been expected based on the foraging behaviour of each predator in isolation (Soluk and Collins 1988; Sih et al. 1998). MPEs can result in either risk reduction or risk enhancement for shared prey species (Billick and Case 1994; Van Son and Thiel 2006). There are various hypotheses regarding the underlying mechanisms driving these two MPE outcomes. Risk reduction, for example, has been predicted to occur when predator-predator interactions lead to reduced foraging rates in one or both predators which ultimately results in lower predation risk for the prey (Sih et al. 1998; Vance-Chalcraft and Soluk 2005; Liu et al. 2017). In contrast, risk enhancement can occur when different predators forage in different habitats, thus reducing refugia for prey, and/or when the defences of prey are inappropriate against some predators (Soluk and Collins 1988; Harvey et al. 2004). If predation risk for mussel prey in the field would have been predicted solely from the prey preferences of both predators in separate experiments, the expectation would have been intense predation pressure on the native *C. meridionalis*, regardless of the proportions in which different prey were offered. However, by considering multiple predators a different conclusion emerges, as the invasive *S. algosus* is as vulnerable to predation as the native *C. meridionalis*.

Accounting for the possible occurrence of MPEs in this system does, therefore, contribute towards a more realistic prediction of what is likely happening in the field. It is important to note that the observed proportions of prey consumed reflect the combined predatory impact of the two native predators, masking the prey preference of individual predator species. When viewed in conjunction with the prey preferences of co-occurring predators, it becomes clear that even though a prey species may appear to be avoided by a specific predator, the overall predatory effect can nonetheless result in strong predation pressure on that prey. For example, in isolated predator experiments *S. algosus* was not the most preferred prey species of either of the two predators, but still experienced strong predation pressure (similar to *C. meridionalis*) when predators co-occurred. Thus, despite previous suggestions that *S. algosus* experiences little to no biotic resistance, this is likely not the case as MPEs can overshadow individual prey preference, ultimately leading to strong predation pressure on a previously avoided invasive prey species. This study thus highlights the importance of accounting for MPEs when attempting to make predictions of the outcomes of predator-prey interactions. Notably, MPEs have not been accounted for in an invasion

context but are clearly important when trying to understand the potential outcomes of prey invasions and the role of predator-driven biotic resistance.

In light of these results it is suggested that future work should incorporate more native predators with overlapping distributions throughout the invasive range of *S. algosus*. In Chapter 2, for example, it was shown that the starfish *Marthasterias africana* also prefers *C. meridionalis*, while avoiding *S. algosus* and *A. atra*. It can therefore be predicted that in communities where *M. africana* is the only predator, there will be no considerable impact on populations of the invasive *S. algosus* and thus little, if any, biotic resistance. Future studies could consider if these effects would be altered if more co-occurring predators are accounted for, as the findings reported in this chapter illustrate that MPEs can influence the potential for biotic resistance. Importantly, it needs to be kept in mind that the direction of this effect will likely be context dependent with previous MPE studies highlighting the importance and interconnectedness of factors such as habitat complexity (Grabowski et al. 2008), variation in prey defenses against different predators (Eklöv and VanKooten 2001), and variation in the behaviour of predators (Harvey et al. 2004).

It is recognized that there were some discrepancies between the field- versus laboratory experiments. Laboratory experiments were performed over the course of multiple days and the field experiment ran for only 12 hours. However, the rapid predatory responses by both predators in the rock pool produced sufficient data to allow for assessment of prey preference and MPEs. Furthermore, whelks were not starved prior to the multiple predator experiment as they were for the isolated predator experiment in the laboratory. However, whelks in the field were not considered to be satiated due to an overall lack of food resources in the rock pool where the field experiment took place. Lastly, it would have been ideal to perform all the experiments in the same setting (i.e. either laboratory or field). However, laboratory experiments were not possible for co-occurring predator trials as space limitations prevented the simultaneous stocking of whelks and rock lobsters at densities in which they occur in the field. To determine the prey preference of predators in isolation, it was important to ensure that there was no interference from other predators. While this could have been achieved through field mesocosm experiments, it was not possible in our study region because of concerns related to safety and the risk of rock lobster poaching.

In conclusion, this study shows that MPEs are present within the communities that contain whelks, rock lobsters, and various co-occurring mussel prey species, including the invasive mussel *S. algosus*. It demonstrates that overall predatory impact of multiple predators can differ from predictions based solely on individual prey preference. In this scenario, MPEs resulted in increased risk for all prey species, including *S. algosus*. This highlights the need for future studies that aim to determine the potential for predator-driven biotic resistance to

account for the potential existence of MPEs and the implications thereof for alien prey invasions.

CHAPTER 4:

Prolonged exposure to *Semimytilus algosus* drives a switch in prey preference by the lobster *Jasus lalandii*

Abstract

The ability of native predators to adapt to novel invasive prey is important not only in terms of the potential for controlling populations of invasive prey species, but also with respect to the persistence of predator populations when faced with an altered prey base. Shifting prey choices of native predators can occur through several mechanisms that may operate over different timescales. Short-term changes in predator feeding behaviour can manifest as a result of continuous exposure to a particular prey, also referred to as conditioning. This study aimed to determine whether the native west coast rock lobster *Jasus lalandii*, is capable of shifting from feeding on its preferred native mussel prey (*Choromytilus meridionalis*) to a novel invasive mussel (*Semimytilus algosus*) through conditioning towards the invasive prey. Wild-caught rock lobsters were fed exclusively on *S. algosus* for a period of four weeks. During this time, the *S. algosus* offered were progressively altered from crushed individuals to fully intact mussels, with only whole mussels offered in the final week. Subsequent laboratory experiments examined the prey preference of conditioned *J. lalandii* by presenting them with a mix of two native (*Aulacomya atra* and *C. meridionalis*) and one invasive mussel species (*S. algosus*) in proportions that they would encounter in the field. Conditioned rock lobsters preferred *S. algosus* while displaying avoidance of the native mussels. This suggests that, as the invasion of *S. algosus* progresses, rock lobsters have the capability to switch their feeding toward this invasive prey and may in fact come to select it over native mussels. Importantly, the results from this study highlight the dynamic nature of predator-prey relationships and demonstrates that the potential for predator-driven biotic resistance against an invasive prey can change through time.

4.1 Introduction

Changes in natural environments, such as those resulting from invasions by alien species, can have a variety of impacts on ecosystems (Blackburn et al. 2014; Jeschke et al. 2014), such as habitat homogenization and the alteration of food webs and nutrient cycling (Simberloff et al. 2013). While it is important to assess these effects, it is equally important to study the potential for adaptation to such disturbances as such information is necessary to understand the long-term consequences of changes to the environment (Phillips and Shine 2004; Berthon 2015). This is particularly relevant in an invasion context as alien species are regarded as a major contributor towards global change (Simberloff et al. 2013). One of the

ways through which such change can be brought about is through disruption of interactions among species (Gallardo et al. 2016), and the way that native species respond and adapt to such disruptions can play an important role in determining the outcome of an invasion (Carlsson et al. 2009).

Alien prey invasions that result in the displacement of competitively inferior native prey can alter the prey base of native predators (Magoulick and Lewis 2002). In such cases, predators that switch toward feeding on novel alien prey may not only exert biotic resistance against these invasions (DeRivera et al. 2005) but can also experience increased fitness compared to those unable to adapt to utilise the new abundant resource (Carlsson et al. 2009). However, native predators may face several challenges when attempting to consume alien prey, including the handling of morphologically novel prey (Cattau et al. 2018), and/or overcoming toxic defence mechanisms of some species (Phillips et al. 2010). The ability of predators to switch to novel or alternative prey becomes especially important when competition for prey resources increases (Gaymer et al. 2001; Albins and Hixon 2008), when prey develop novel defence mechanisms (Rowland et al. 2017), and/or when prey populations face threats that might result in population declines (Carlsson et al. 2009).

Adaptation in response to a novel prey source may operate through different mechanisms and over different timescales. This includes contemporary evolution (Carroll et al. 2005), social transmission (Brown and Laland 2003; Tinker et al. 2009), and conditioning (Hughes and O'Brien 2001; Diller et al. 2014). Adaptive responses in native species that develop through contemporary evolution do so over several generations (Carrol et al. 2008), e.g. evolutionary changes that appear in less than a few hundred years (Stockwell et al. 2003). Such adaptation can be influenced by several factors, including genetic variance, generation time, population structure, time since colonisation, and the phylogenetic distance between native and invasive communities (Carroll et al. 2005; Strauss et al. 2006), all of which have the potential to act alone or in combination. This has been illustrated in the case of native soapberry bugs (*Leptocoris tagalicus*) that have evolved longer mouthparts to predate on the seeds of invasive balloon vine (*Cardiospermum grandiflorum*) in as short a timeframe as 30 – 40 years (Carroll et al. 2005). By killing seeds before dehiscence, native soapberry bugs could potentially reduce the rate of balloon vine spread throughout its introduced range (Carroll et al. 2005). Similarly, a recent study by Cattau et al. (2018) has shown that a native predator, the endangered snail kite (*Rostrhamus sociabilis*), has rapidly increased its bill- and body size following the invasion of an invasive prey, the island apple snail (*Pomacea maculata*). Not only is this novel prey substantially larger than the native snails upon which snail kites normally feed, but it is also more abundant (Cattau et al. 2018). Consequently, snail kite nestlings with the altered traits are more likely to survive their first year. The rapid morphological changes in

this native predator has been attributed to a high level of phenotypic plasticity (Cattau et al. 2018).

Predators can also respond to novel prey over shorter timeframes. Social transmission of novel information related to the location or handling of novel prey (Palameta and Lefebvre 1985), for example, can rapidly spread through a population (Page and Ryan 2006). In most instances, experienced individuals (demonstrators) will be observed by inexperienced conspecifics (observers) (Brown and Laland 2003), which enhances the likelihood or rate of adaption to the novel food source (Palameta and Lefebvre 1985). Social transmission is also useful when predators are faced with spatial and temporal variation in the availability of different prey types (Page and Ryan 2006). A study by Page and Ryan (2006) demonstrated that novel foraging behaviour can rapidly spread through a population of predatory bats (*Trachops cirrhosus*) through social transmission. In this study, some individuals were conditioned to associate a novel acoustic prey cue (toad calls) with a profitable food type. These individuals were then paired with bats lacking prior experience with this acoustic cue or food. By observing the experienced bats, inexperienced individuals rapidly displayed the same foraging behaviour. Similar behaviours have been documented in various taxa, including fish, birds and mammals (Brown and Laland 2003), but studies considering social transmission as a strategy through which native predators can adapt to a novel invasive prey are presently lacking.

The final mechanism through which predators can rapidly adapt to a novel prey is through conditioning. Various factors have been proposed to influence conditioning, including past experience with prey (Hughes and Dunkin 1984b; Jackson and Underwood 2007), frequency of prey encounters (Tinker et al. 2009; Rowland et al. 2017), and handling capabilities of the predator (Hughes and O'Brien 2001). In the western Atlantic, Caribbean and Gulf of Mexico, invasions by lionfish (*Pterois volitans, Pterois miles*) have resulted in an altered prey base for native predators. This has been attributed to high rates of lionfish predation on native prey, subsequently increasing competition between the invasive lionfish and native predators for shared prey (Albins and Hixon 2008). Research has shown that some native predators (e.g. Nassau grouper and nurse sharks) have started to incorporate invasive lionfish into their diets despite their venomous spines (Diller et al. 2014). In this case, adaptation to the novel invasive prey has been attributed to conditioning, that likely took place when these predators initially consumed lionfish injured during culling operations in the region (Diller et al. 2014). It is also considered that learning to consume novel prey may occur more readily in predators that are generalists than in those that are specialist feeders who are often adapted to handling specific prey types (Hughes and O'Brien 2001). The variety of feeding mechanisms used by generalist predators might further be advantageous when novel prey bares morphological similarity with familiar native prey, as predicted by skill transfer theory (Hughes

and O'Brien 2001). It has been shown, for example, that European shore crabs (*Carcinus maenas*) conditioned to certain prey types are better able to consume novel but morphologically similar prey when compared to crabs conditioned on morphologically different prey (Hughes and O'Brien 2001). The concept of conditioning in native predators as an adaptive response to invasions by alien prey, however, is a topic that has received very little research attention (but see Bartsch et al. 2005; Robbins et al. 2013).

In Chapters 2 and 3, it was revealed that three generalist predators, west coast rock lobster *Jasus lalandii,* spiny starfish *Marthasterias africana*, and whelks of the genus *Burnupena*, select for a scarce native mussel prey (*Choromytilus meridionalis*) despite a greater abundance of invasive mussels (*Mytilus galloprovincialis* and *Semimytilus algosus*). It has already been demonstrated that the avoidance of invasive prey is not related to the relative structure or energetic content of the different mussel prey (Chapter 2) but can most likely be explained by unfamiliarity with this novel prey (e.g. in terms of chemical cues and taste). In Chapter 1, it was established that *S. algosus* is abundant in subtidal habitats on the west coast of South Africa and on the Cape Peninsula. As this invasion progresses, it is expected that native subtidal predators will be increasingly faced with altered prey communities, in which *S. algosus* will be a dominant species. This is because 1) this species faces little predation pressure and 2) the selective feeding on native mussels is expected to reduce inter-specific competition faced by *S. algosus*, potentially facilitating its dominance.

Based on this information, the aim of this chapter was to determine whether the lack of selection of *S. algosus* by the native predator *J. lalandii* can be overcome through continuous exposure to the invasive prey (i.e. conditioning). As a result of its weak shell strength *S. algosus* requires less energy to consume, and this together with the fact that it offers the highest energetic reward of all the mussel species (Chapter 2), suggests that from an energetic budget perspective, this species should represent the optimal prey choice. It was therefore predicted that, given isolated and continuous exposure to *S. algosus*, rock lobsters would come to prefer this invasive prey over native mussel species (*A. atra* and *C. meridionalis*).

4.2 Methodology

Specimen collection

All mussels were collected from the same sites as those in Chapter 2 and had shell lengths of 20 – 30 mm. Rock lobsters (70 - 100 mm carapace length) were collected from Kalk Bay Harbour on the south coast of South Africa (Fig. 2.1, Chapter 2). This site was chosen as *Semimytilus algosus* only recently spread to the south coast (Chapter 2) and thus predators occurring in this region would have had little to no exposure to this species.

Phase 1: Predator conditioning

The first phase of experiments served as a conditioning period during which individual *J. lalandii* were exposed only to *S. algosus*. This ensured that *S. algosus* would be continuously encountered by *J. lalandii*, thereby promoting familiarity with this particular prey without the influence of any other prey species. Conditioning took place in the field in order to ensure that rock lobsters were exposed to cues from *S. algosus* in the presence of other naturally occurring cues. Following collection, rock lobsters were transported to False Bay Yacht Club (FBYC) in Simon's Town (Fig. 2.1, Chapter 2). Here, 20 rock lobsters were kept in separate cages (0.045 m^3). These cages were covered with plastic mesh (0.5 x 0.5 cm) to exclude other potential prey organisms from entering the cages. A seven-day starvation period was used to allow for acclimatization to the cages and to ensure that conditioning toward *S. algosus* commenced at equal hunger levels for all rock lobsters. This was followed by four weeks of conditioning during which *J. lalandii* was fed with only *S. algosus* in crushed and whole forms. The total number of mussels given to each lobster per week was kept constant throughout the conditioning phase (n = 40). The ratio of crushed to whole mussels was however progressively adjusted, with only whole mussels offered in the final week (Table 4.1).

Table 4.1: Ratios of *Semimytilus algosus* in different forms as adjusted over the predator conditioning phase.

Week	Crushed : Whole
1	30 : 10
2	20 : 20
3	10 : 30
4	0 : 40

Phase 2: Determining the effect of conditioning on prey preference

To determine whether conditioning can alter the prey preference of *J. lalandii* from *C. meridionalis* toward *S. algosus,* mussel preference of conditioned rock lobsters (this chapter) was contrasted with non-conditioned rock lobsters (Chapter 3). Experimental details described in Chapter 3 apply to this chapter, except that before an assessment of prey preference was made, lobsters were conditioned for four weeks as described above. Assessment of prey preference took place in the laboratory where lobsters were kept in individual 38l tanks in aerated seawater (13^0C) with daily water changes. A seven-day starvation period was once again employed to standardize hunger levels and allow for acclimatization to the new surroundings. Rock lobsters were presented with different mussel prey in varying proportions that represented different invasion scenarios, i.e. a current and future diet (see Chapter 3, section 3.2 for details). Daily checks of experimental tanks included the identification, removal and replacement of consumed mussels in order to maintain constant proportions of the different prey species throughout the experiment.

Statistical analyses

In feeding trials with conditioned and non-conditioned lobsters, some individuals moulted or did not feed at all, an indication that lobsters are soon to moult (Mayfield et al. 2000a). These individuals were therefore excluded from statistical analyses. Consequently, although trials were begun with 10 replicates for each diet for both conditioned and non-conditioned lobsters, analyses of conditioned lobsters included six replicates for the current diet treatment and eight for the future diet, while for non-conditioned lobster analyses were conducted on seven replicates in the current diet and eight in the future diet. Chesson (1978) selectivity indices were calculated for each prey species (native *A. atra* and *C. meridionalis* and invasive *S. algosus*) in each diet treatment (current, future) (see section 2.2). Chesson index values were arcsine transformed prior to analyses in order to be released from a proportional nature. Several comparisons were used to establish whether prey selection differed between conditioned and non-conditioned lobsters. Firstly, Friedman's ANOVAs were used to assess differences in the Chesson index values for different mussel prey species in each diet treatment for both conditioned and non-conditioned lobsters. These were followed by Conover post hoc tests (Conover 1980) to detect differences between Chesson index values of prey species within each diet treatment. Secondly, to establish whether conditioning altered selection of a particular prey species, the Chesson index values of each prey species as selected by conditioned and non-conditioned lobsters in each diet treatment were compared. After meeting the assumptions of normality and equal variances, these comparisons were made using T-tests with a Bonferroni correction to account for multiple tests.

4.3 Results

No mortality was recorded for lobsters during the conditioning phase. All mussels in the holding tanks survived throughout the duration of the laboratory experiment, confirming that mussel mortality in experimental tanks was a result of predation by *Jasus lalandii* and no other confounding factors. For non-conditioned lobsters, prey species had significantly different Chesson index values in the current (χ^2_2= 7.153, p = 0.027, Fig. 4.1a) and future (χ^2_2 = 7.517, p = 0.023, Fig. 4.1b) diet treatments. Notably, the native mussel *Choromytilus meridionalis* had positive selection values in both the current and future diet treatments, regardless of the fact that this species was always offered in lower abundance than either *Aulacomya atra* (current diet) or *Semimytilus algosus* (future diet).

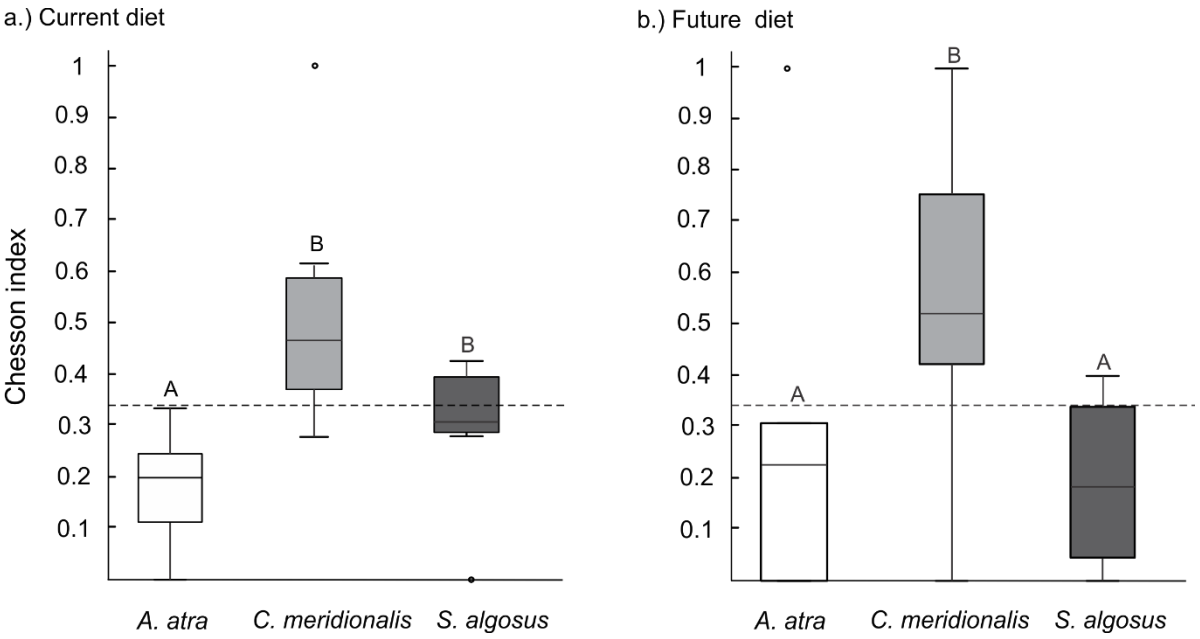

Figure 4.1: Median (interquartile range, minimum and maximum) Chesson selectivity indices for three prey species (*Aulacomya atra*, *Choromytilus meridionalis*, and *Semimytilus algosus*) as predated upon by non-conditioned *Jasus lalandii* in (a) current and (b) future diet treatments. Dots represent outliers. Boxes with different letters differ significantly (Conover post hoc with Bonferroni correction). Values above the line = positive selection (preference), on the line = neutral selection, below the line = negative selection (avoidance).

Prey species consumed by lobsters that were conditioned toward *S. algosus* also had significantly different Chesson index values in the current (X^2_2 = 6.869, p = 0.032) and future (X^2_2 = 9.867, p = 0.007) diet treatments. It is notable that conditioning toward *S. algosus* resulted in significantly greater Chesson index values of this species compared to the native *A. atra* and *C. meridionalis* and that this result persisted regardless of the proportions in which the three mussel species were offered in the current and future diets (Fig. 4.2).

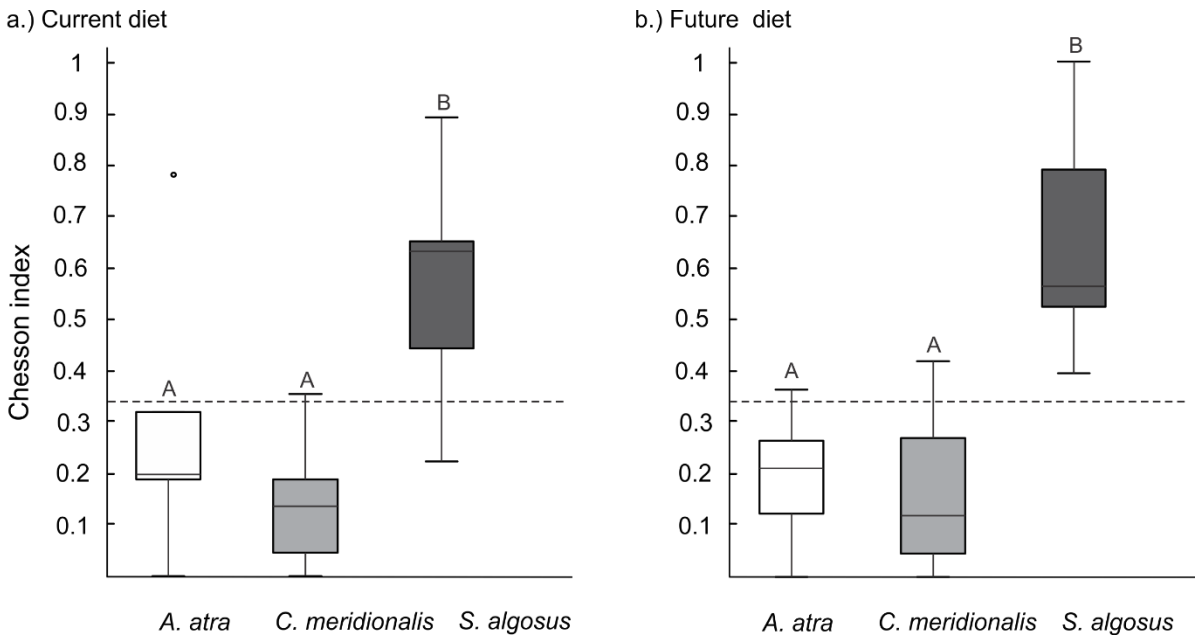

Figure 4.2: Median (interquartile range, minimum and maximum) Chesson selectivity indices for three prey species (*Aulacomya atra*, *Choromytilus meridionalis*, and *Semimytilus algosus*) as predated upon by conditioned *Jasus lalandii* in (a) current and (b) future diet treatments. Dots represent outliers. Boxes with different letters differ significantly (Conover post hoc test with Bonferroni correction). Values above the line = positive selection (preference), on the line = neutral selection, below the line = negative selection (avoidance).

Prey species-specific comparisons of Chesson index values further revealed notable changes in selection between conditioned and non-conditioned lobsters. For the invasive *S. algosus*, Chesson index values were significantly greater in conditioned lobsters, which was true in both the current (T_{11} = 2.402, p = 0.035; Fig. 4.3a) and future diet treatments (T_{14} = 4.084, p = 0.001; Fig. 4.3b). This was accompanied by a decreased preference for the native *C. meridionalis*, as reflected by lower Chesson index values for this species in conditioned lobsters in both the current (T_{11} = 3.115, p = 0.009; Fig. 4.3a) and future diets (T_{14} = 2.656, p = 0.019; Fig.4.3b). Lastly, Chesson index values for the native *A. atra* remained low regardless of predator conditioning in both the current (T_{11} = 0.706, p = 0.495; Fig. 4.3a) and future diet treatments (T_{14} = 0.221, p = 0.828; Fig.4.3b).

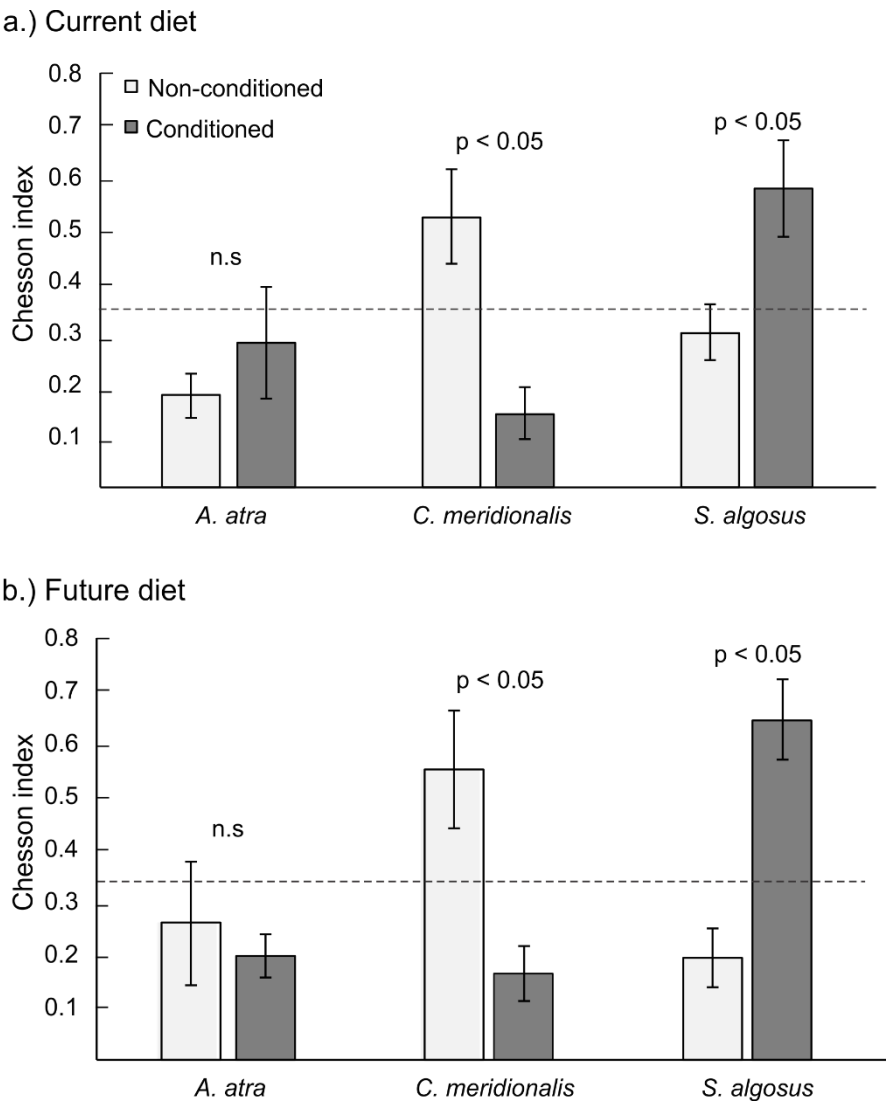

Figure 4.3: Species-specific comparisons between Chesson selectivity index values (mean ± SE) for prey (native *Aulacomya atra* and *Choromytilus meridionalis*, invasive *Semimytilus algosus*) as predated upon by non-conditioned and conditioned *Jasus lalandii* in the (a) current and (b) future diet treatments. Values above the dotted line = positive selection (preference), values on the line = neutral selection and values below the line = negative selection (avoidance).

4.4 Discussion

Native predators could be expected to shift towards feeding on novel prey when such prey has low associated search- and handling times, and when it offers higher energetic rewards compared to other prey, as predicted by classic foraging theory (Stephens and Krebs 1986). However, despite the obvious benefits that novel prey may present to predators, shifts to feeding on such prey are not necessarily immediate (Carroll et al. 2005). The ability of native predators to adapt to an altered prey base as a result of prey invasions is important not only in terms of biotic resistance, but also in ensuring that predators will be able to incorporate such prey should native prey end up being displaced (Strauss et al. 2006; Berthon 2015; Cattau et al. 2018). The results presented in this chapter indicate that a native predator (*Jasus lalandii*)

can incorportate the invasive mussel *Semimytilus algosus* through prolonged exposure, which can lead to a preference for the invasive prey despite initial avoidance.

Lobsters possess sensitive chemoreceptors that play a crucial role in the detection of prey (Derby et al. 2001). Such detection has been shown to be complex, with lobsters being able to differentiate between species-specific prey cues and subsequently decide whether or not to respond to such cues with predatory pursuit or avoidance (Derby et al. 2001). The decision to pursue a specific prey species is known to be influenced by the lobsters' past experience with the prey, with frequent exposure often promoting a predatory response (Derby and Atema 1981; Derby et al. 2001). Continuous exposure can lead to the development of a chemical 'search image' for a specific prey, which can subsequently improve the ability to locate and ingest that prey (Derby and Atema 1981). A study by Derby and Atema (1981) assessed several predatory behaviours of American clawed lobster (*Homarus americanus*) before and after exposure to one of two mussel species (*Modiolus modiolus* and *Mytilus edulis*). Following repeated exposure to the cues of each prey, lobsters displayed markedly increased responsiveness to the respective prey cues on which they had been conditioned. Such chemoreceptive plasticity has been shown to be important in animals that are omnivorous, long-lived, and found in various types of habitat, all of which can lead to variation in prey availability (Derby et al. 2001). Thus, even though lobsters are known as generalist predators, variability in prey preference at an individual level can be large. In addition, it has been suggested that lobsters may have a genetic predisposition to act on chemical cues from prey that are profitable (Daniel and Bayer 1987). The ability to develop a chemical 'search image' for a particular prey (promoted through continuous exposure) can in itself be viewed as a mechanism that enhances the detection and intake of profitable prey. Indeed, previous attempts of conditioning to prey species of poor quality has been unsuccessful (Daniel and Bayer 1987), strongly suggesting that lobsters can differentiate between profitable and non-profitable prey (Daniel and Bayer 1987; Derby et al. 2001).

The findings of this chapter align with the above descriptions of lobster feeding behaviour. Chapters 2 and 3 examined the prey preference of *J. lalandii* from two different populations, with both exhibiting a preference toward the native mussel *Choromytilus meridionalis*. Although *C. meridionalis* is not the most abundant subtidal mussel species, it is easier to consume than the more abundant *A. atra*, owing to weaker adductor muscle strength and less complex shell structure (Chapter 2). With the invasive *S. algosus* requiring even less force to break than *C. meridionalis* and offering a greater energetic reward (Chapter 2), it would theoretically represent the most profitable prey choice for *J. lalandii*. Therefore, the preference for *S. algosus* documented after conditioning most likely developed due to *J. lalandii* learning to recognise a novel prey cue and associating this cue with a profitable prey. This could ultimately result in lobsters actively seeking out this prey, despite the presence of *A. atra* and

C. meridionalis. In this study, preference toward *S. algosus* developed following exclusive exposure to this species. If other prey species were in the vicinity during the conditioning phase, development of this preference may have been slower. However, given the strong switch of preference from *C. meridionalis* to *S. algosus,* and the favourable characteristics of the latter as prey, it is likely that as *S. algosus* becomes abundant, preference for this prey will develop.

This chapter suggests that even though a native predator may initially avoid an invasive prey, it can over time become preferred through conditioning. Furthermore, it emphasizes the fact that biotic resistance should not be measured through a single observation in time (Carroll et al. 2005). As the invasion of *S. algosus* progresses, there is potential for native predators such as *J. lalandii* to adapt and switch towards feeding on this abundant invasive prey, even if they avoid it at first. In this case, predation will probably have a limiting rather than an excluding effect on the invasive prey, as the preference toward this prey was not immediate. The chances for exclusion through predation is likely to be greater if native predators rapidly switch to feeding on invasive prey upon their introduction (Carlsson et al. 2009), thereby potentially preventing the establishment and spread of the alien species. Notably, along the South African coastline, populations of *J. lalandii* have been in steep decline due to overfishing and illegal poaching activities (Mead et al. 2013). Thus, any future potential biotic resistance from *J. lalandii* against *S. algosus* could be moderated by human impacts on lobster populations. This serves to highlight the importance of an ecosystem approach to managing threats in marine ecosystems.

CHAPTER 5:

Assessing characteristics of native predators and invasive prey that are important in determining the outcome of predator driven biotic resistance

Abstract

Predator-driven biotic resistance is known to be more effective in aquatic than terrestrial systems. However, there is little consensus in the literature about when such resistance can be expected to succeed or fail. This chapter reviewed case-studies that investigated interactions between native marine predators and alien prey, with the aim of establishing which characteristics are important in determining the outcome of such interactions. Four potential biotic resistance outcome scenarios were identified, with these scenarios progressing from a state of no resistance to successful resistance when an alien species is successfully excluded from the native community. For each case-study, the presence or absence of characteristics of native predators and invasive prey were identified. The outcome of the native predator-alien prey interaction was then assigned to one of the four biotic resistance outcome scenarios, based on the conclusions made by the study. Multivariate statistics were used to examine potential differences in the suites of characteristics typifying each of the four outcome scenarios. These characteristics were found to differ significantly among scenarios with failure of predator-driven biotic resistance occurring in cases where the alien prey typically had high fecundity, high recruitment and substantial dispersal potential. Conversely, successful biotic resistance was related to the characteristics of native predators including high abundance, strong predation pressure on alien prey, coupled with high feeding rates. Importantly, this research emphasizes the need to integrate information from both trophic groups to strengthen predictions about the outcomes of novel predator-prey interactions.

5.1 Introduction

The concept of biotic resistance dates back to the influential work by Elton (1958) and was initially founded on the notion that communities with high diversity should be less susceptible to invasions by alien species. In such communities, strong competition often results in limited resources (Stachowicz et al. 2002), and species that thrive are likely equipped with traits that enable them to efficiently utilise key resources (Tilman 1999). In addition, such communities are often relatively stable and experience reduced temporal variation in community properties such as biomass fluctuations (Stachowicz et al. 2007). As a result, the stronger competition, limited resources, and stable community properties in such communities leave few niches open for an alien species to occupy. However, this relatively broad perception

of biotic resistance has since evolved and presently includes several mechanisms through which resistance can be exerted (Levine et al. 2004; Kimbro et al. 2013).

The three main mechanisms of biotic resistance are now recognised as competition, herbivory, and predation (Pimm 1989; Tilman 1999; Stachowicz et al. 2002), with each shown to be context dependent and variable among ecosystems (Dunstan and Johnson 2004; Rius et al. 2014). In terrestrial systems, competition-driven resistance can be a significant force acting to limit invasions by alien producers with the strength of this resistance known to increase with increasing native producer diversity (Levine et al. 2004). Overall, competition-driven resistance is most effective when resources such as food and space are limited (Stachowicz and Byrnes 2006). In contrast, resistance through herbivory is thought to be most effective in freshwater systems (Alofs and Jackson 2014). The generalist nature of many native freshwater herbivores has been suggested to facilitate incorporation of novel invasive plants into their diets (Alofs and Jackson 2014). Indeed, in a study by Morrison and Hay (2011), the majority of herbivores examined showed a strong preference for invasive compared to native plants. High feeding rates coupled with a preference for invasive plants, as has been reported in the case of two native crayfishes (*Procambarus spiculifer* and *Procambarus acutus*; Parker and Hay 2005), infers high potential for strong biotic resistance in communities where such predators are abundant. In marine systems, the dominant mechanism through which biotic resistance has been recorded to operate is predation (see reviews by Weiss 2011; Kimbro et al. 2013; Prior et al. 2015; Papacostas et al. 2017). At a local scale, marine communities are often not saturated in terms of species richness (Witman et al. 2004), and thus competition-driven biotic resistance is less likely to operate (Kimbro et al. 2013). Predator-driven biotic resistance may become especially important in subtidal habitats as they are permanently submerged and not subjected to the physiological forces (e.g. wave action and aerial exposure) of intertidal systems that can affect predation pressure.

The effectiveness of predator-driven biotic resistance has been suggested to be influenced by many factors, including life-history and behavioural characteristics of native predators (Carlsson et al. 2009), alien prey (Branch and Steffani 2004; Rius et al. 2014), and habitat features (Byers 2002b). For example, the degree of predation pressure from native crab predators on the invasive varnish clam *Nuttallia obscurata* varies according to substrate characteristics (Byers 2002b; Dudas et al. 2005). A study by Dudas et al. (2005) demonstrated that when two native crabs, *Cancer magister* and *Cancer productus*, were offered a mix of native littleneck clams and invasive varnish clams in a substratum with limited depth, both predators preferred the invasive *N. obscurata*. This was attributed to the invasive prey being easier to access and consume and therefore energetically more profitable compared to the native clam. However, when the clams were presented in a substratum with unlimited depth, invasive varnish clams burrowed significantly deeper than native clams, resulting in a shift in

the prey preference by one of the native predators (*C. productus*). This finding explains the abundance of *N. obscurata* in the field, which often occurs in the high intertidal zones characterised by a sandy substrate. Tethering experiments have shown that without this predation refuge, *N. obscurata* would not be a successful invasive species due to high predation pressure by native crab predators (Byers 2002b).

Additionally, the foraging decisions made by native predators can be influenced by other factors such as the length of time that a predator is exposed to a particular prey (Carroll et al. 2005; Carlsson et al. 2009). Alien prey species can be novel in various ways, including taste (Carlsson et al. 2009). In Chapter 4, for example, it was found that the prey preference of the rock lobster *Jasus lalandii* can switch from the native black mussel *Choromytilus meridionalis* to the invasive mussel *Semimytilus algosus* if the lobster is exposed only to the invasive prey for a prolonged period. Foraging decisions can also be influenced by the presence of other predators, as established in Chapter 3. Here, prey selection by rock lobsters became more varied in the presence of *Burnupena* whelks, and the co-occurrence of these two predators resulted in increased risk for all mussel species, including *S. algosus.* While this is not likely to result in effective biotic resistance, it demonstrates the importance of accounting for co-occurring predators in biotic resistance studies.

When considering alien prey, there are several life-history characteristics that may influence the degree to which biotic resistance affects invasive success. Prey species with multiphasic life cycles, for example, can be susceptible to different mechanisms of biotic resistance as they progress through different life stages. This has been shown in species that occupy distinct trophic niches at different life stages, such as the widespread invasive ascidian *Ciona intestinalis* (Collin et al. 2013). A study by Rius et al. (2014) demonstrated that biotic resistance through competition and predation operate interchangeably to affect the survival of *C. intestinalis* at different stages of its life cycle. Here it was found that predation was important in larval and juvenile stages, while competition with native ascidians act during fertilisation and adulthood (Rius et al. 2014). In other cases, high reproductive output of alien prey can completely overwhelm all effects of predation. Along the South African coastline, for example, the native predatory whelk, *Trochia cingulata*, prefers the invasive mussels *Mytilus galloprovincialis* and *S. algosus* (Alexander et al. 2015a). However, despite this preference, consumption by *T. cingulata* has little impact on population size (Branch and Steffani 2004; Alexander et al. 2015a) due to the extremely high recruitment rates of the invasive mussels (Robinson et al. 2007b; Zeeman et al. 2018).

It has been suggested that for predation-driven biotic resistance to manifest, the rate of consumption needs to outstrip that of reproductive output and recruitment (Twardochleb et al. 2012). Notably, there are few documented cases where such resistance has led to the complete elimination of an alien prey species. However, the recording of biotic resistance

eliminating a newly introduced species is expected to be rare, as this would require knowledge of the arrival of an alien species before they have established. Considering the difficulties associated with early detection of marine alien species (Collin et al. 2013), this could bias the literature toward cases where predator-driven biotic resistance fails or only limits, but does not eliminate, alien prey populations. However, when considering cases where such resistance significantly impacts the success of alien prey, the importance of this regulating force is clear (Harding et al. 2003). For example, the European shore crab *Carcinus maenas* is invasive in several regions around the world and is recognised as having negative impacts in invaded communities (Walton et al. 2002; Garbary et al. 2014). However, along the east coast of the United States, predation from the native blue crab *Callinectes sapidus* has been credited as the major driver of the southern range limit of the invader (DeRivera et al. 2005). Several factors have been suggested to play a role in this successful biotic resistance: importantly, native blue crabs consume *C. maenas* despite the presence of alternative prey items, their consumption rate is high, and there is a strong relationship between *C. sapidus* abundance and *C. maenas* mortality. Furthermore, DeRivera et al. (2005) suggest that temperature may also play a role in this resistance, as warmer conditions in more southerly habitats correlate with *C. sapidus* abundance and predatory activities (e.g. feeding behaviour and rate). This case-study highlights that when key factors align, predation-driven biotic resistance can be a dominant regulating force of invasive prey populations.

Results from previous studies demonstrate that predator-driven biotic resistance can be context dependent, influenced by characteristics of alien prey (Branch and Steffani 2004; Rius et al. 2014), native predators (Carlsson et al. 2009) and competitors (Rius et al. 2014), and in some cases, environmental conditions (Byers 2002b). Previous work aimed at predicting the outcomes of invasions have made efforts to identify traits generally associated with successful invaders (Williamson and Fitter 1996; Swart et al. 2018), while others consider attributes of native communities (Case 1990). However, varying outcomes suggest that these factors cannot be considered separately, and rather all potential role players in an invasion scenario need to be accounted for to improve the accuracy of predictions of the outcomes of alien prey invasions.

In this chapter, a novel approach was used to identify the factors that influence the success or failure of predator-driven biotic resistance in marine systems. Specifically, this chapter aimed to determine which characteristics of alien prey and native predators govern the outcomes of interactions between native predators and alien prey. Secondly, the ability of this approach to predict biotic resistance outcomes was assessed by applying it to the subtidal invasion of *S. algosus* in South Africa. As *S. algosus* is dominant in this habitat (Chapter 1) and appears to be avoided by multiple native predators (Chapters 2, 3), it was predicted that this alien prey experiences little to no predator-driven biotic resistance.

5.2 Methodology

Literature review

Published literature investigating interactions between alien prey and native predators was identified in March 2019 through online data bases (*Google Scholar*, *Web of Science*) using the following search terms: 'biotic resistance', 'marine', 'native predator/s', 'invasive', 'alien', 'exotic', 'regulation', 'exclusion', 'limit', 'restrict', as well as the names of well-known marine invasive prey species. Case-studies that met the following criteria were used for identifying potentially important characteristics of alien prey and native predators: (1) predators were native to the study region; (2) information was provided on predator selection of alien prey, either through manipulative experiments or observational data; (3) information was available on predator abundance in the study region; (4) the authors provided conclusions addressing the potential for predator-driven biotic resistance in the region of study. Prey invasions across all stages of invasion were considered, i.e. naturalised and invasive alien prey (Robinson et al. 2016).

A list of characteristics of alien prey and native predators thought to be of importance in determining the potential for predator-driven biotic resistance was compiled *a priori*. For alien prey that are likely to experience invasive success, these characteristics were: high reproductive output, high recruitment, high fecundity, rapid growth rate, high dispersal potential, inducible defences (i.e. plastic responses in response to different predators), high propagule pressure, gregarious behaviour, and prey that experience refuge from predation. Characteristics of native predators thought to promote effective biotic resistance were: high abundance, high feeding rates, predators with generalist feeding tendencies and strong selection of alien prey (which could be a result of preference for alien over native prey, or of random selection that nonetheless results in high consumption rates of alien prey).Four main biotic resistance outcome scenarios were identified through the literature review (Table 5.1). These scenarios range from no resistance owing to a complete lack of predation pressure (Scenario 1) to successful biotic resistance that can limit or exclude alien prey (Scenario 4).

Table 5.1: The four proposed biotic resistance outcome scenarios as identified from case-studies that examined interactions between native predators and invasive prey.

Scenario	Description
S1	No alien prey are consumed by native predators. Increased potential for enemy release (Keane and Crawley 2004) and facilitation of prey invasion.
S2	Little predation pressure, but not strong enough to have a measurable impact on alien prey populations. Predators may prefer native prey but importantly can consume alien prey if no other alternatives are available.
S3	Considerable predation pressure, but not enough to limit or exclude alien prey. Predators exert strong effects on alien prey populations through preference for these prey or an overall high but random consumption of various prey species within the community.
S4	Successful biotic resistance. Predation pressure on alien prey is sufficient to either limit the distribution of or completely exclude the alien prey from the community.

Sufficient information for eight of the 13 *a priori* alien prey and native predator characteristics could be found in the case-studies (Table 5.2). Subsequently, the presence or absence of each of these characteristics was identified in each case-study (Appendix 5.1 Table 5.1.1), and when not all the characteristics were described in the case-study itself the required information was sourced from other publications (see Appendix 5.1 for full reference list). As some life-history characteristics can vary regionally (Mackie and Schloesser 1996), when sourcing additional information priority was given to studies conducted in the same region as the case-study.

Inclusion of the Semimytilus algosus *case-study*

To assess the ability of this approach to successfully characterise the various outcomes of interactions between native predators and alien prey (Table 5.1), the South African invasion of *Semimytilus algosus* in subtidal habitats was included as a case-study. The characteristics of *S. algosus* as a prey and native subtidal predators (Table 5.2) were scored using information obtained throughout this thesis (Appendix 5.1 Table 5.1.1). Additional experiments were also conducted to supplement the scoring of these characteristics. This included the growth rate of *S. algosus* in a subtidal habitat, and the feeding rate of an important subtidal mussel predator, the rock lobster *Jasus lalandii* (established through functional response experiments) (Appendix 5.2). Based on the findings of Chapters 1, 2 and 3 it was predicted that the biotic resistance outcome of this case-study would be Scenario 2 (little predation pressure but ineffective resistance).

Table 5.2: Important characteristics identified through a review of case-studies that examined the interaction between alien prey and native predators.

Characteristic	Description
Alien prey	
1. Gregarious behaviour	A tendency to form groups or clumps. Such behaviour may be advantageous in terms of limiting accessibility or increase handling difficulty by predators.
2. High fecundity	Fecundity that imparts a competitive advantage. When fecundity of an alien species has been described as substantially higher than that of its native comparator, or when it allows for the successful occupation of an unfilled niche in the invaded community.
3. High recruitment	High recruitment into the adult population. Notably when recruitment exceeds that of native competitors and is high enough to overwhelm predation effects.
4. High dispersal potential	Planktonic larvae with a long pelagic larval phase (> 1 week) that can enable localised establishment and spread of at least $10^0 – 10^2$ m (as per Simkanin et al. 2013); or prey with high mobility (e.g. fish).
5. Predation refuge	Toxic defences (e.g. organisms that produce toxic secondary metabolites); behavioural defences (e.g. autotomizing body parts when attacked to enable escape); structural defences (e.g. shells too strong for predators to break); rapid growth that allows prey to escape the 'window of vulnerability'; isolation from predators through artificial structures (e.g. fouling communities on floating docks)
Native predators	
6. Strong predation pressure on alien prey	When alien prey is preferred over native prey or when prey selection is random but nonetheless results in strong overall predation pressure on alien prey.
7. High feeding rate	Predator feeding rates reported as having regulating effects on prey populations. Such regulating effects can manifest in various ways including (1) predators demonstrating a type-II functional response (Hassell 1978), i.e. high consumption rates of prey when at low densities and (2) predation by single or multiple predators. In cases where predation efforts from a suite of predators were considered but species-specific feeding rates were not given, the description of overall feeding rates were used.
8. High abundance	Always numerically dominant within the native community. Not applicable to predators with seasonal peaks in abundance.

Statistical analyses

A PERMANOVA was used to assess differences in the suites of characteristics among case studies representing the four invasion scenarios. SIMPER was used to identify the characteristics that contributed most to the similarity within each scenario. All statistical analyses were conducted in PRIMER (version 6) software package.

5.3 Results

The literature review yielded a total of 43 case-studies including the one of the *Semimytilus algosus* invasion in subtidal habitats along the South African coastline (Appendix 5.1 Table 5.1.1). Some case-studies recorded multiple biotic resistance outcomes (e.g. comparative studies of biotic resistance in various habitats), resulting in the following sample sizes (n) for each scenario: S1 = 15, S2 = 17, S3 = 7, S4 = 16. The relevant information regarding the *S. algosus* case-study was based primarily on results gained throughout this thesis. The suites of characteristics present in the four outcome scenarios differed significantly when the *S. algosus* cases study was excluded (PERMANOVA Pseudo-F =19.018, p = 0.001) and this pattern remained the same when this case study was included (PERMANOVA Pseudo-F = 19.25, p = 0.001; Fig. 5.1). Pairwise comparisons revealed significant differences among all scenarios ($p < 0.01$) except between Scenario 3 and 4 ($p = 0.119$). The prediction that *S. algosus* would experience little predation pressure and hence ineffective resistance (i.e. Scenario 2) was confirmed as this case-study grouped with other Scenario 2 outcomes (Fig. 5.1).

SIMPER revealed that Scenario 1 (i.e. no predation-driven resistance) and Scenario 2 (i.e. little predation pressure and ineffective resistance) were typified by prey characteristics (Table 5.3). High prey fecundity was most important in defining Scenario 1, while in Scenario 2 high levels of prey recruitment and high prey dispersal capabilities, coupled with high prey fecundity were important (Table 5.3). In contrast, Scenarios 3 and 4 were defined by predator characteristics. In Scenario 3 (strong predation pressure but ineffective resistance), strong predation pressure on alien prey was the defining characteristic (Table 5.3). Lastly, Scenario 4 (strong predation pressure and successful resistance) was defined by predator characteristics of which a high feeding rate and high predator abundance were the most important (Table 5.3).

Table 5.3: SIMPER results of the relative contributions made by alien prey and native predator characteristics to the overall similarity of four biotic resistance outcome scenarios.

Scenario	Characteristic	% Contribution	% Cumulative
Scenario 1	High fecundity	27.04	27.04
(Average similarity = 76.96)	High recruitment	23.50	50.54
	Gregarious behaviour	23.13	73.67
	Predation refuge	17.16	90.84
Scenario 2	High fecundity	21.48	21.48
(Average similarity = 81.92)	High recruitment	21.48	42.95
	High dispersal potential	21.48	64.43
	Gregarious behaviour	15.98	80.41
	High abundance	9.64	90.05
Scenario 3	Strong predation pressure on alien prey	22.01	22.01
(Average similarity = 76.81)	High abundance	16.17	38.18
	Gregarious behaviour	15.28	53.45
	High fecundity	14.77	68.22
	High dispersal potential	14.77	82.99
	High recruitment	10.14	93.13
Scenario 4	High feeding rate	22.07	22.07
(Average similarity = 81.98)	High abundance	22.07	44.14
	Strong predation pressure on alien prey	19.35	63.50
	High fecundity	14.01	77.51
	Gregarious behaviour	8.26	85.77
	High dispersal potential	7.59	93.36

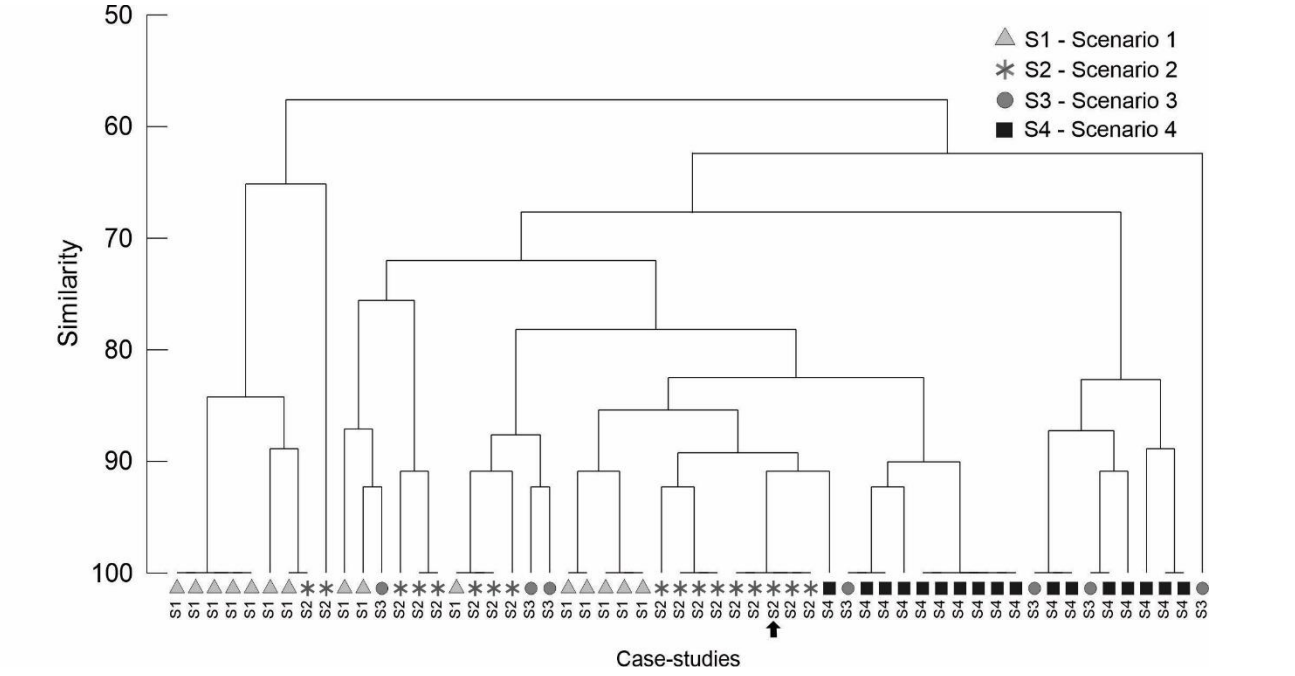

Figure 5.1: Cluster dendrogram of case-studies assigned to the four different biotic resistance outcome scenarios (Scenario 1 – total lack of predation pressure; Scenario 2 – little predation pressure but ineffective resistance; scenario 3 – Strong predation pressure but ineffective resistance; Scenario 4 – strong predation pressure and effective resistance). The case-study of the South African *Semimytilus algosus* invasion was hypothesized to represent a Scenario 2 outcome and was found to group among other Scenario 2 case-studies (black arrow).

5.4 Discussion

There are numerous factors that can affect the outcomes of predator-prey interactions (Grabowski 2004; Ferrari et al. 2011; Maraffini and Geller 2015). This is equally true for novel interactions that occur between native predators and alien prey (Carlsson et al. 2009). Identification of factors that influence the outcomes of such interactions can provide an improved understanding regarding predator-driven biotic resistance and when it can be expected to operate effectively against invasions by alien prey. This study found that the outcomes of marine predator-driven biotic resistance depend on the characteristics of both alien prey and native predators and that where native predators are most likely to exclude alien prey from a community, they tend to (1) be abundant within the community, (2) strongly select for alien prey, and (3) exhibit high feeding rates (Fig. 5.2). In contrast the degree of biotic resistance failure (Table 5.1) was found to depend on the combination of prey characteristics and the absence of dominant predator characteristics. High fecundity, recruitment and dispersal potential of alien prey in combination

with the absence of either strong predation pressure, high predator abundance and/or high feeding rates by native predators, were found to likely result in biotic resistance failure.

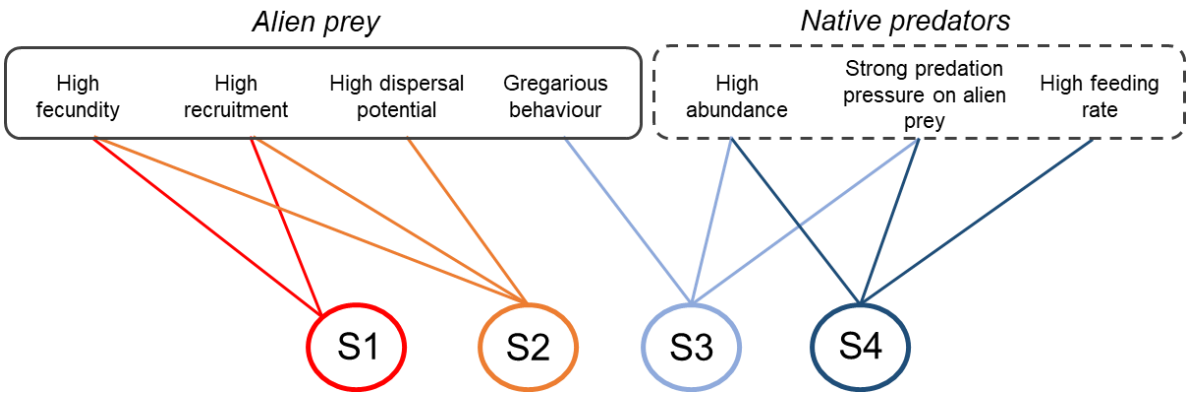

Figure 5.2: Alien prey (solid black line) and native predator (dotted black line) characteristics that contributed at least 50% to the overall similarity within each biotic resistance scenario (S1-S4). As the defining characteristics of Scenario 3 (strong predation pressure but ineffective resistance) and Scenario 4 (strong predation pressure and effective resistance) did not differ significantly (ANOSIM, $p > 0.05$), they are both depicted in shades of blue. Note that 'predation refuge' as a characteristic of prey is not depicted in this diagram, as it was not identified as a defining characteristic for any scenario.

To evaluate the accuracy with which alien prey and native predator characteristics were ascribed to the different biotic resistance outcomes, the case-study of *Semimytilus algosus* was included as a 'test case'. This species has been observed in high densities in intertidal (de Greef et al. 2013; Zeeman et al. 2018) and subtidal (Chapter 1) habitats. It has been shown to have high fecundity and recruitment (Zeeman et al. 2018), high dispersal potential (Narváez et al. 2006) and although native predators are capable of consuming *S. algosus*, it is unlikely that it will result in effective resistance as native mussels remain their preferred prey (but see Chapter 4 for prey switching in rock lobster *Jasus lalandii*). The grouping of this case-study among other Scenario 2 cases demonstrates the ability of this approach to successfully characterise predator-driven biotic resistance outcomes.

Previous studies investigating the impacts of invasive species on natives (generally invasive predators and native prey) have been met with scrutiny for focussing on single aspects of predator or prey behaviour (for example see Dick et al. 2017; Vonesh et al. 2017). Indeed, there are many different opinions regarding the best predictive tools for understanding impact which has relevance in the context of biotic resistance (Bomford et al. 2010). For example,

Twardochleb et al. (2012) suggests that biotic resistance will be effective when the feeding rates of native predators outstrip that of alien prey reproduction but fails to mention prey preference or the influence of alternative prey. In contrast, numerous publications predict that a preference for an alien over a native prey is key for effective resistance (Carlsson et al. 2009; Ejdung et al. 2009; Epelbaum et al. 2009; Shinen et al. 2009). Studies more focussed on alien prey predict that species with high propagule pressure (Hollebone and Hay 2007), with r-selected life-histories (Morton 1997), or that are pre-adapted to the climatic conditions of the introduced region (Bomford et al. 2010) have high probabilities of invasion success, irrespective of native predator abundance or behaviour. The lack of consensus in the field is clear. Nonetheless, research considering single aspects of native predators and alien prey behaviour and demographics remains valuable, as it provides useful information that can be integrated as done in this study. Importantly, this chapter highlights that incorporating both alien prey and native predator characteristics, and the varying combinations in which they can occur, can provide meaningful insight into the observed outcomes of alien prey-native predator interactions.

The lack of a significant difference between Scenario 3 (strong predation pressure but ineffective resistance) and Scenario 4 (strong predation pressure and effective resistance) may be explained by a current bias in published information. This is reflected in the fact that Scenario 3 outcomes were documented in only seven studies, with other Scenarios recorded in more than double the number of studies. Thus, the ability to separate Scenario 3 from Scenario 4 may improve as more studies document this outcome.

There are several aspects that may affect predator-prey dynamics that could not be accounted for in this study. Propagule pressure (i.e. the number and frequency of alien individuals released into a region to which they are not native (Lockwood et al. 2005)) is one such factor, although substantial propagule pressure has been shown capable of overcoming predation-driven biotic resistance in marine systems (Hollebone and Hay 2007; Clark and Johnston 2009). Unfortunately, this aspect of invasions can be difficult to quantify in the marine environment (Simkanin et al. 2017), resulting in an overall paucity of information regarding propagule pressure of marine alien species. As such, propagule pressure could not be incorporated into this study, although the influence thereof should not be disregarded. There are also factors that can alter the foraging behaviour of native predators, such as adaptation toward novel alien prey and non-consumptive effects (NCEs). NCEs are behavioural changes of one organism in response to cues from another, also referred to as inducible defences or trait-mediated effects (Abrams 2007; Bourdeau et al. 2010; Turner et al. 2017). As some native predators adapt to feeding on novel

alien prey over time, this process holds important implications for future biotic resistance potential (Carroll et al. 2005). In aquatic environments, waterborne cues from predators detected by prey may result in increased defensive/avoidance behaviour, which may lead to decreased feeding time, thereby having potential effects on growth (Jermacz and Kobak 2017), reproduction (Preisser and Bolnick 2008), and recruitment (Bertolini et al. 2019). In contrast, if alien prey can detect and appropriately respond to cues from novel native predators it can increase the chances of invasion success (Grason and Miner 2012). The extent to which NCEs affect prey has been suggested to decrease with increasing prey density, as a high prey density reduces individual predation risk (McCoy 2007). As such, the responses of alien prey to native predators during the initial stages of an invasion may be important due to typically low numbers of individuals at this stage (Grason and Miner 2012). However, this is a concept that has only recently started to gain research attention, especially in marine invasion ecology (Grason and Miner 2012) but see Phillips and Shine (2004), Carroll et al. (2005), and Cattau et al. (2018) for non-marine examples.

In light of the results of this study, it is suggested that greater insight into the context dependency associated with the outcomes of biotic interactions could be gained by accounting for the characteristics of the biota involved. Within the milieu of predator-driven biotic resistance, it is clear that the nature of both local predators and alien prey are important in determining if biotic resistance will manifest or not. The fact that abundant native predators with high feeding rates are characteristic of successful predator-driven biotic resistance highlights the need to conserve fully functioning marine systems. Reduced or depleted predator populations as a result of pressures such as over-harvesting may leave these ecosystems more vulnerable to invasions by alien prey.

SYNTHESIS

Marine ecosystems are among the most heavily invaded systems on earth (Ruiz et al. 1999; Castorani and Hovel 2016) but our understanding of the determinants of invasion success and the impacts of invasions lags behind that of other systems (Chan and Briski 2017; Papacostas et al. 2017). This thesis addressed important knowledge gaps related to the invasion of the Chilean mussel *Semimytilus algosus* along the South African coast and used this invasion to investigate novel interactions between native subtidal predators and invasive prey.

The South African west coast was invaded by *S. algosus* approximately 10 years ago (de Greef et al. 2013). Since then, studies conducted in the region have considered its intertidal distribution (de Greef et al. 2013), impacts on native community composition (Sadchatheeswaran et al. 2015, 2018), competitive abilities (via resource acquisition) (Alexander et al. 2015b), life-history strategies (Zeeman et al. 2018), and its role as a novel prey for the whelk *Trochia cingulata* (Alexander et al. 2015a). Although this work has been important in understanding the invasion of *S. algosus* in the intertidal region, there has been no research considering the subtidal invasion of *S. algosus*. As the abiotic and biotic characteristics of intertidal and subtidal environments differ substantially, it is likely that so too will the invasion dynamics in these two systems.

Differences in the inter- and subtidal invasions of *S. algosus* were reflected in the results of Chapter 1, where surveys of mussels conducted in both environments revealed that the species is well established in the subtidal, although the intertidally dominant *Mytilus galloprovincialis* was virtually absent. Notably, although the native mussel *Aulacomya atra* remains dominant in the subtidal, *S. algosus* has spread around the biogeographic break of Cape Point and is expected to continue spreading eastwards. The ability of *S. algosus* to proliferate in the subtidal was further evidenced by its condition being comparable to native mussels and the fact that in this habitat it reaches sizes double that previously reported in the region (de Greef et al. 2013). These findings provide the first insight into invasion patterns of *S. algosus* in subtidal communities, but also reveal important avenues for future research. Key questions that still remain to be addressed include how *S. algosus* might affect subtidal mussel bed community composition, what the mechanisms of potential coexistence and/or competition are between *S. algosus* and native comparators, and what the potential distribution range of this species is along the south coast.

Investigations into subtidal community dynamics focussed on novel interactions between *S. algosus* as a novel invasive prey and its native predators were pursued in Chapters 2, 3 and

4. Predation is a major structuring force of subtidal communities (Connell 1972; Menge 2002) and the foraging decisions made by native predators when faced with novel alien prey can have important implications for the outcomes of an invasion (Sousa et al. 2009; Carlsson et al. 2011; Joyce et al. 2019). Avoidance by predators can indirectly facilitate the invasion success of an alien prey, while strong predation pressure can regulate or even completely exclude such alien species (DeRivera et al. 2005). To begin to address the potential for predator-driven biotic resistance against *S. algosus* in the subtidal, the prey preferences of three subtidal predators were explored. Spiny starfish *Marthasterias africana* (Chapter 2), whelks of the genus *Burnupena* (Chapter 3) and west coast rock lobster *Jasus lalandii* (Chapter 2, 3) all preferred the same native mussel *Choromytilus meridionalis*, even when *S. algosus* was the most abundant prey species on offer. These findings challenge traditional views of optimal foraging theory, as *S. algosus* was the most profitable prey choice in terms of handling difficulty and energetic reward. These results suggest that contrary to predictions based on the theory of optimal foraging (Hughes 1979), native predators may avoid profitable novel food choices as a result of unfamiliarity. This presents an interesting avenue for future research, as the exact drivers behind this avoidance remains unknown.

Prey selection can, however, be dynamic and change as a result of various factors. One such factor is the presence of other predators. In Chapter 3 rock lobsters displayed large discrepancies in prey selection depending on the presence or absence of *Burnupena* whelks. Previous work has shown that *J. lalandii* can suffer extreme predation from these whelks when the latter is present in very high densities (Barkai and Branch 1988a; Barkai and McQuaid 1988). The results of Chapter 3 suggest that *J. lalandii* perceives high densities of *Burnupena* as a potential threat, as rock lobsters avoided the prey on which *Burnupena* was feeding. The densities of the respective predators at which the switch from predator to prey occurs is yet to be assessed but this interesting interaction appears to have important implications for the predation risk of their shared prey. Indeed, Chapter 3 revealed that the co-occurrence of whelks and rock lobsters resulted in increased predation risk for all prey, including *S. algosus*. It will be meaningful for future studies to incorporate a larger suite of co-occurring native predators, as this can further increase our understanding of the implications of multiple predators in an invasive prey context.

Prey selection can also vary depending on the past feeding experiences of native predators. If a predator consistently feeds on a particular prey species for an extended time, it may encourage future selection for the same species (i.e. predator conditioning; Hughes and Dunkin 1984b; Tinker et al. 2009). Chapter 4 demonstrated that this is possible in the rock lobster

J. lalandii, as following conditioning this predator selected for *S. algosus* over all native mussel prey. The fact that a preference for this prey could develop over the course of a few weeks suggests that *J. lalandii* would not be threatened by decreases in native mussel abundance, should the invasion of *S. algosus* result in significant decreases in the abundance of these native prey. Future studies can look to determine whether other native predators will exhibit similar prey switching behaviour in response to prolonged exposure to a novel, initially avoided alien prey species. Doing so will not only improve our understanding of predator adaptations in the face of changing prey communities, but also enable the identification of predator species that are more likely to be severely affected by a changing prey base.

The findings of this thesis emphasize the high degree of context dependency in the potential impacts that native predators can have on alien prey. The invasive mussel *S. algosus* is not likely to experience significant biotic resistance from native predators along the west coast or in False Bay. Effective resistance is contingent upon predators that are abundant, have high feeding rates and demonstrate strong predation pressure (e.g. via selective predation) on alien prey (Chapter 5). These findings highlight that putting conservation measures in place to safeguard populations of native predators in the face of threats such as over-exploitation and pollution may well offer a viable approach for regulating alien prey invasions. Predators have long been recognised as being important for sound ecosystem functioning, and this thesis has highlighted that this role can be particularly important within an invasion context.

Appendix 5.1

Table 5.1.1: Case-studies investigating interactions between alien prey and native predators and scoring of characteristics related each trophic group. Presence of a characteristic is denoted by 1 while absence is denoted by 0.

#	Case-study reference	Outcome	Alien prey	Native predator	Characteristic	Result	Reference
1.1	Alexander et al. (2015).	S2	*Mytilus galloprovincialis*	*Trochia cingulata*	Gregarious behaviour	1	Liu et al. (2012).
					High fecundity	1	de Greef et al. (2013)
					High recruitment	1	Branch and Steffani (2004).
					High dispersal	1	McQuaid and Phillips (2000).
					Predation refuge	0	Branch and Steffani (2004).
					Predaion pressure	1	Alexander et al. (2015).
					High feeding rate	0	Alexander et al. (2015).
					High predator abundance	0	Robinson et al. (2015).
1.2	Alexander et al. (2015).	S2	*Semimytilus algosus*	*Trochia cingulata*	Gregarious behaviour	1	Liu et al. (2012).
					High fecundity	1	Zeeman et al. (2018).
					High recruitment	1	Zeeman et al. (2018).
					High dispersal	1	Narváez et al. (2006).
					Predation refuge	0	Alexander et al. (2015).
					Predation pressure	1	Alexander et al. (2015).
					High feeding rate	0	Alexander et al. (2015).
					High predator abundance	0	Robinson et al. (2015).
2	Brousseau et al. (2008).	S2	*Hemigrapsus sanguineus*	*Fundulus spp.*	Gregarious behaviour	0	
					High fecundity	1	Dauvin et al. (2009).
					High recruitment	1	McDermott (1998).

					High dispersal	1	Park et al. (2004).
					Predation refuge	1	Brousseau et al. (2008).
					Predation pressure	0	Brousseau et al. (2008).
					High feeding rate	1	Brousseau et al. (2008).
					High predator abundance	1	Brousseau et al. (2008).
3	Castilla et al. (2004).	S3	*Pyura praeputialis*	multiple	Gregarious behaviour	1	Rius et al. (2010).
					High fecundity	0	Manríquez and Castilla (2010).
					High recruitment	1	Castilla et al. (2004).
					High dispersal	0	Castilla et al. (2004).
					Predation refuge	0	Castilla et al. (2004).
					Predation pressure	1	Castilla et al. (2004).
					High feeding rate	0	Castilla et al. (2004).
					High predator abundance	1	Castilla et al. (2004).
4	Cheng and Hovel (2010).	S4	*Musculista senhousia*	*Panulirus interruptus, Pteropurpura festiva*	Gregarious behaviour	1	Cheng and Hovel (2010).
					High fecundity	1	Crooks (2001).
					High recruitment	1	Crooks (2001).
					High dispersal	1	Crooks (1996).
					Predation refuge	0	Crooks (1996).
					Predation pressure	1	Cheng and Hovel (2010).
					High feeding rate	1	Cheng and Hovel (2010).
					High predator abundance	1	Cheng and Hovel (2010).
5	DeRivera et al. (2005).	S4	*Carcinus maenas*	*Callinectes sapidus*	Gregarious behaviour	0	
					High fecundity	1	Yamada (2001).
					High recruitment	0	DeRivera et al. (2005).
					High dispersal	1	Colnar and Landis (2007).
					Predation refuge	0	DeRivera et al. (2005).
					Predation pressure	1	DeRivera et al. (2005).

					High feeding rate	1	DeRivera et al. (2005).
					High predator abundance	1	DeRivera et al. (2005).
6	Diller et al. (2014).	S3	*Pterois spp.*	*Epinephelus striatus, Ginglymostoma cirratum*	Gregarious behaviour	1	Hunt and Yamada (2003).
					High fecundity	1	Côté et al. (2013).
					High recruitment	1	Diller et al. (2014).
					High dispersal	1	Ahrenholz and Morris (2010).
					Predation refuge	1	Albins (2013).
					Predation pressure	1	Diller et al. (2014).
					High feeding rate	1	Diller et al. (2014).
					High predator abundance	0	Diller et al. (2014).
7.1	Dumont et al.(2011a).	S4	*Ciona intestinalis*	multiple	Gregarious behaviour	1	Dumont et al.(2011a).
					High fecundity	1	Carver et al. (2003).
					High recruitment	1	Dumont et al.(2011a).
					High dispersal	0	Howes et al. (2007).
					Predation refuge	0	Dumont et al.(2011a).
					Predation pressure	1	Dumont et al.(2011a).
					High feeding rate	1	Dumont et al.(2011a).
					High predator abundance	1	Dumont et al.(2011a).
7.2	Dumont et al.(2011a).	S1	*Ciona intestinalis*	multiple	Gregarious behaviour	1	Dumont et al.(2011a).
					High fecundity	1	Carver et al. (2003).
					High recruitment	0	Dumont et al.(2011a).
					High dispersal	0	Howes et al. (2007).
					Predation refuge	1	Dumont et al.(2011a).
					Predation pressure	1	Dumont et al.(2011a).
					High feeding rate	1	Dumont et al.(2011a).
					High predator abundance	0	Dumont et al.(2011a).

8.1	Dumont et al. (2011b).	S1	*Bugula neritina*	no urchins, *Rhyncocinetes typus,* some blennid fishes	Gregarious behaviour	1	Keough (1984).
					High fecundity	1	Dumont et al. (2011b).
	soft sediment pilings, away from rocky reef				High recruitment	1	Cifuentes et al. (2010).
					High dispersal	0	Keough (1984).
					Predation refuge	1	Dumont et al. (2011b).
					Predation presure	1	Dumont et al. (2011b).
					High feeding rate	1	Dumont et al. (2011b).
					High predator abundance	0	Dumont et al. (2011b).
8.2	Dumont et al. (2011b).	S4	*Bugula neritina*	*Tetrapygus niger* *Rhyncocinetes typus*	Gregarious behaviour	1	Keough (1984).
					High fecundity	1	Dumont et al. (2011b).
	community with benthic predators				High recruitment	0	Dumont et al. (2011b).
					High dispersal	0	Keough (1984).
					Predation refuge	0	Dumont et al. (2011b).
					Predation pressure	1	Dumont et al. (2011b).
					High feeding rate	1	Dumont et al. (2011b).
					High predator abundance	1	Dumont et al. (2011b).
9.1	Forrest et al. (2013).	S4	*Didemnum vexillum*	*Patriella regularis*, *Evechinus chloroticus*, *Coscinasterias muricata*, *Turbo smaragdus*, *Cryptoconchus porosus*, Paguridae	Gregarious behaviour	1	Forrest et al. (2013).
					High fecundity	1	Forrest et al. (2013).
					High recruitment	1	Bullard et al. (2007).
					High dispersal	0	Fletcher et al. (2013).
					Predation refuge	0	Forrest et al. (2013).
					Predation pressure	1	Forrest et al. (2013).
					High feeding rate	1	Forrest et al. (2013).
					High predator abundance	1	Forrest et al. (2013).
9.2	Forrest et al. (2013).	S1	*Didemnum vexillum*	*Patriella regularis*, *Evechinus chloroticus*, *Coscinasterias muricata*,	Gregarious behaviour	1	Forrest et al. (2013).
					High fecundity	1	Forrest et al. (2013).
					High recruitment	1	Bullard et al. (2007).

				Turbo smaragdus, *Cryptoconchus porosus*, Paguridae	High dispersal	0	Fletcher et al. (2013).
					Predation refuge	1	Forrest et al. (2013).
					Predation pressure	0	Forrest et al. (2013).
					High feeding rate	0	Forrest et al. (2013).
					High predator abundance	0	Forrest et al. (2013).
10	Freudendahl et al. (2010).	S4	*Ensis americanus*	*Somateria mollissima*, *Haemotopus ostralegus*	Gregarious behaviour	0	Freudendahl et al. (2010).
					High fecundity	0	Armonies and Reise (1999).
					High recruitment	0	Armonies and Reise (1999).
					High dispersal	1	Armonies and Reise (1999).
					Predation refuge	0	Freudendahl et al. (2010).
					Predation pressure	1	Freudendahl et al. (2010).
					High feeding rate	1	Freudendahl et al. (2010).
					High predator abundance	1	Freudendahl et al. (2010).
11.1	Gestoso et al. (2014).	S2	*Xenostrobus securis*	*Carcinus maenas*, *Nucella lapillus*	Gregarious behaviour	1	Liu et al. (2012).
					High fecundity	1	Garci et al. (2007).
					High recruitment	1	Gestoso et al. (2014).
					High dispersal	1	Garci et al. (2007).
					Predation refuge	1	Gestoso et al. (2014).
					Predation pressure	0	Gestoso et al. (2014).
					High feeding rate	0	Gestoso et al. (2014).
					High predator abundance	0	Gestoso et al. (2014).

11.2	Gestoso et al. (2014).	S4	*Xenostrobus securis*	*Carcinus maenas*, *Nucella lapillus*	Gregarious behaviour	1	Liu et al. (2012).
					High fecundity	1	Garci et al. (2007).
					High recruitment	0	Gestoso et al. (2014).
					High dispersal	1	Garci et al. (2007).
					Predation refuge	0	Gestoso et al. (2014).
					Predation pressure	1	Gestoso et al. (2014).
					High feeding rate	1	Gestoso et al. (2014).
					High predator abundance	1	Gestoso et al. (2014).
12	Grey (2010).	S1	*Botrylloides violaceus*	Various grazers (chitons, flatworms, gastropods)	Gregarious behaviour	1	Grey (2010).
					High fecundity	1	Bock et al. (2011).
					High recruitment	1	Grey (2010).
					High dispersal	0	Saito et al. (1981).
					Predation refuge	0	Grey (2010).
					Predation pressure	0	Grey (2010).
					High feeding rate	1	Grey (2010).
					High predator abundance	1	Grey (2010).
13	Harley et al. (2013).	S4	*Littorina littorea*	*Pisaster ochraceus*, *Pycnopodia helianthoides*	Gregarious behaviour	0	Harley et al. (2013).
					High fecundity	0	Harley et al. (2013).
					High recruitment	0	Harley et al. (2013).
					High dispersal	1	Johannesson (1992).
					Predation refuge	0	Harley et al. (2013).
					Predation pressure	1	Harley et al. (2013).
					High feeding rate	1	Harley et al. (2013).
					High predator abundance	1	Harley et al. (2013).
14	Hollebone and Hay (2007).	S2	*Petrolisthes armatus*	*Panopeus herbstii*	Gregarious behaviour	1	Wassick et al. (2017).
					High fecundity	1	Wassick et al. (2017).
					High recruitment	1	Hollebone and Hay (2007).
					High dispersal	1	Gore (1972).

					Predation refuge	0	Hollebone and Hay (2007).
					Predation pressure	0	Hollebone and Hay (2007).
					High feeding rate	1	Hollebone and Hay (2007).
					High predator abundance	1	Hollebone and Hay (2007).
15	Hosia and Titelman (2010).	S2	*Mnemiopsis leidyi*	*Cyanea capillata*	Gregarious behaviour	0	Reeve et al. (1989).
					High fecundity	1	Reeve et al. (1989).
					High recruitment	1	Van Ginderdeuren et al. (2012).
					High dispersal	1	Bolte et al. (2013).
					Predation refuge	0	Hosia and Titelman (2010).
					Predation pressure	0	Hosia and Titelman (2010).
					High feeding rate	1	Hosia and Titelman (2010).
					High predator abundance	1	Hosia and Titelman (2010).
16	Hunt and Yamada (2003).	S4	*Carcinus maenas*	*Cancer productus*	Gregarious behaviour	0	Hunt and Yamada (2003).
					High fecundity	1	Yamada (2001).
					High recruitment	0	Hunt and Yamada (2003).
					High dispersal	1	Colnar and Landis (2007).

					Predation refuge	0	Hunt and Yamada (2003).
					Predation pressure	1	Hunt and Yamada (2003).
					High feeding rate	1	Hunt and Yamada (2003).
					High predator abundance	1	Hunt and Yamada (2003).
17	Joyce et al. (2019).	S2	*Crassostrea gigas*	*Asterias rubens, Carcinus maenas*	Gregarious behaviour	1	Reise et al. (2017).
					High fecundity	1	Helm et al. (2004).
					High recruitment	1	Diederich (2005).
					High dispersal	1	Reise et al. (2017).
					Predation refuge	0	Joyce et al. (2019).
					Predation pressure	0	Joyce et al. (2019).
					High feeding rate	1	Joyce et al. (2019).
					High predator abundance	1	Joyce et al. (2019).
18	Kinney et al. (2019).	S2	*Petrolisthes armatus*		Gregarious behaviour	1	Wassick et al. (2017).
					High fecundity	1	Wassick et al. (2017).
					High recruitment	1	Hollebone and Hay (2007).
					High dispersal	1	Gore (1972).
					Predation refuge	1	Kinney et al. (2019).
					Predation pressure	0	Kinney et al. (2019).
					High feeding rate	1	Kinney et al. (2019).
					High predator abundance	1	Kinney et al. (2019).
19	Kushner and Hovel (2006).	S3	*Musculista senhousia*	*Pteropurpura festiva*	Gregarious behaviour	1	Cheng and Hovel (2010).
					High fecundity	1	Crooks (2001).
					High recruitment	1	Crooks (2001).

					High dispersal	1	Crooks (1996).
					Predation refuge	1	Kushner and Hovel (2006).
					Predation pressure	1	Kushner and Hovel (2006).
					High feeding rate	0	Kushner and Hovel (2006).
					High predator abundance	1	Kushner and Hovel (2006).
20	Lages et al. (2010).	S1	*Turbastraea* spp.	Generalist fish	Gregarious behaviour	1	Creed and De Paula (2007).
					High fecundity	1	Creed and De Paula (2007).
					High recruitment	1	Creed and De Paula (2007).
					High dispersal	0	Creed and De Paula (2007).
					Predation refuge	1	Lages et al. (2010).
					Predation pressure	0	Lages et al. (2010).
					High feeding rate	1	Lages et al. (2010).
					High predator abundance	1	Lages et al. (2010).
21	League-Pike and Shulman (2009).	S3	*Carcinus maenas*	*Homarus americanus, Cancer borealis*	Gregarious behaviour	0	Hunt and Yamada (2003).
					High fecundity	1	Yamada (2001).
					High recruitment	0	Hunt and Yamada (2003).
					High dispersal	1	Colnar and Landis (2007).

					Predation refuge	0	League-Pike and Shulman (2009).
					Predation pressure	1	League-Pike and Shulman (2009).
					High feeding rate	1	League-Pike and Shulman (2009).
					High predator abundance	1	League-Pike and Shulman (2009).
22	López et al. (2010).	S2	*Isognomon bicolor*	*Stramonita haemastoma, Trachypollia nodulosa*	Gregarious behaviour	1	López et al. (2010).
					High fecundity	1	Breves-Ramos et al. (2010).
					High recruitment	1	Breves-Ramos et al. (2010).
					High dispersal	1	Breves-Ramos et al. (2010).
					Predation refuge	1	López et al. (2010).
					Predation pressure	0	López et al. (2010).
					High feeding rate	0	López et al. (2010).
					High predator abundance	1	López et al. (2010).
23	Ma and Purcell (2005).	S4	*Moerisia lyonsi*	*Chrysaora quinquecirrha*	Gregarious behaviour	0	
	High salinity (>10)				High fecundity	High fecundity	Ma and Purcell (2005).
					High recruitment	1	Wintzer et al. (2011).
					High dispersal	1	Ma and Purcell (2005).
					Predation refuge	0	Ma and Purcell (2005).
					Predation pressure	1	Ma and Purcell (2005).
					High feeding rate	1	Ma and Purcell (2005).

					High predator abundance	1	Ma and Purcell (2005).
24	Ma and Purcell (2005).	S1	*Moerisia lyonsi*		Gregarious behaviour	0	
					High fecundity	1	Ma and Purcell (2005).
	low salinity (<10)				High recruitment	1	Wintzer et al. (2011).
					High dispersal	1	Ma and Purcell (2005).
					Predation refuge	1	Ma and Purcell (2005).
					Predation pressure	0	Ma and Purcell (2005).
					High feeding rate	0	Ma and Purcell (2005).
					High predator abundance	0	Ma and Purcell (2005).
25	Marshall (2009).	S4	*Musculista senhousia*	*Thais gradata*	Gregarious behaviour	1	Cheng and Hovel (2010).
					High fecundity	0	Marshall (2009).
					High recruitment	0	Marshall (2009).
					High dispersal	1	Crooks (1996).
					Predation refuge	0	Marshall (2009).
					Predation pressure	1	Marshall (2009).
					High feeding rate	1	Marshall (2009).
					High predator abundance	1	Marshall (2009).
26	Mitchem et al. (2007).	S2	*Perna viridis*	*Callinectes sapidus, Panulirus argus*	Gregarious behaviour	1	Rajagopal et al. (2006).
					High fecundity	1	Barber et al. (2005).
					High recruitment	1	Bayne (1976).
					High dispersal	1	Siddal (1980).
					Predation refuge	0	Mitchem et al. (2007).
					Predation pressure	0	Mitchem et al. (2007).
					High feeding rate	1	Mitchem et al. (2007).
					High predator abundance	1	Mitchem et al. (2007).
27	Moreira et al. (2012).	S1	*Turbastraea* spp.	Various generalist predators	Gregarious behaviour	1	Creed and De Paula (2007).

					High fecundity	1	Creed and De Paula (2007).
					High recruitment	1	Creed and De Paula (2007).
					High dispersal	0	Creed and De Paula (2007).
					Predation refuge	1	Moreira et al. (2012).
					Predation pressure	0	Moreira et al. (2012).
					High feeding rate	1	Moreira et al. (2012).
					High predator abundance	1	Moreira et al. (2012).
28.1	Mumby et al. (2011).	S3	*Pterois spp.*	Grouper	Gregarious behaviour	1	Hunt et al. (2019).
	Inside reserve, large grouper population				High fecundity	1	Côté et al. (2013).
					High recruitment	1	Diller et al. (2014).
					High dispersal	1	Ahrenholz and Morris (2010).
					Predation refuge	0	Mumby et al. (2011).
					Predation pressure	1	Mumby et al. (2011).
					High feeding rate	1	Mumby et al. (2011).
					High predator abundance	1	Mumby et al. (2011).
28.2	Mumby et al. (2011).	S2	*Pterois spp.*	Grouper	Gregarious behaviour	1	Hunt et al. (2019).
	Outside reserve, small grouper population				High fecundity	1	Côté et al. (2013).
					High recruitment	1	Diller et al. (2014).
					High dispersal	1	Ahrenholz and Morris (2010).
					Predation refuge	0	Mumby et al. (2011).
					Predation pressure	1	Mumby et al. (2011).
					High feeding rate	1	Mumby et al. (2011).
					High predator abundance	0	Mumby et al. (2011).

29	Needles et al. (2015).	S1	*Watersipora subtorquata*	*Pisaster spp., Enhydra lutris nereis*	Gregarious behaviour	1	Piola and Johnston (2009).
					High fecundity	1	Piola and Johnston (2009).
					High recruitment	1	Piola and Johnston (2009).
					High dispersal	0	Needles et al. (2015).
					Predation refuge	0	Needles et al. (2015).
					Predation pressure	0	Needles et al. (2015).
					High feeding rate	1	Needles et al. (2015).
					High predator abundance	1	Needles et al. (2015).
30.1	Parry (2017). <15 m depth	S3	*Asterias amurensis*	*Coscinasterias muricata*	Gregarious behaviour	1	Ross et al. (2002).
					High fecundity	1	Byrne et al. (1997).
					High recruitment	0	Parry (2017).
					High dispersal	1	Barker and Nichols (1983).
					Predation refuge	0	Parry (2017).
					Predation pressure	1	Parry (2017).
					High feeding rate	1	Parry (2017).
					High predator abundance	1	Parry (2017).
30.2	Parry (2017). >15 m depth	S1	*Asterias amurensis*	*Coscinasterias muricata*	Gregarious behaviour	1	Ross et al. (2002).
					High fecundity	1	Byrne et al. (1997).
					High recruitment	1	Parry (2017).
					High dispersal	1	Barker and Nichols (1983).
					Predation refuge	1	Parry (2017).
					Predation pressure	0	Parry (2017).
					High feeding rate	0	Parry (2017).
					High predator abundance	0	Parry (2017).

31	Pintor and Byers (2015).	S2	*Petrolisthes armatus*	*Panopeus herbstii*	Gregarious behaviour	1	Wassick et al. (2017).
					High fecundity	1	Wassick et al. (2017).
					High recruitment	1	Hollebone and Hay (2007).
					High dispersal	1	Gore (1972).
					Predation refuge	0	Pintor and Byers (2015).
					Predation pressure	0	Pintor and Byers (2015).
					High feeding rate	1	Pintor and Byers (2015).
					High predator abundance	1	Pintor and Byers (2015).
32	Purcell et al. (2001).		*Mnemiopsis leidyi*		Gregarious behaviour	0	Reeve et al. (1989).
					High fecundity	1	Reeve et al. (1989).
					High recruitment	1	Van Ginderdeuren et al. (2012).
					High dispersal	1	Bolte et al. (2013).
					Predation refuge	0	Purcell et al. (2001).
					Predation pressure	0	Purcell et al. (2001).
					High feeding rate	0	Purcell et al. (2001).
					High predator abundance	0	Purcell et al. (2001).
33	Reusch (1998).	S4	*Musculista senhousia*	*Pteropurpura festiva*	Gregarious behaviour	1	Cheng and Hovel (2010).
					High fecundity	1	Crooks (2001).
					High recruitment	1	Reusch (1998).
					High dispersal	1	Crooks (1996).
					Predation refuge	0	Reusch (1998).
					Predation pressure	1	Reusch (1998).
					High feeding rate	1	Reusch (1998).
					High predator abundance	1	Reusch (1998).

34	Robinson et al. (2015).	S2	*Balanus glandula*	*Trochia cingulata, Burnupena lagenaria*	Gregarious behaviour	1	Wu (1981).
					High fecundity	1	Newman and Abbott (1980).
					High recruitment	1	Gaines et al. (1985).
					High dispersal	1	Gaines et al. (1985).
					Predation refuge	1	Robinson et al. (2015).
					Predation pressure	0	Robinson et al. (2015).
					High feeding rate	0	Robinson et al. (2015).
					High predator abundance	1	Robinson et al. (2015).
35.1	Rogers et al. (2016).	S4	*Botrylloides violaceus*	various benthic predators (chitons, crabs, starfish, urchins)	Gregarious behaviour	1	Grey (2010).
					High fecundity	1	Bock et al. (2011).
					High recruitment	1	Grey (2010).
					High dispersal	0	Saito et al. (1981).
					Predation refuge	0	Rogers et al. (2016).
					Predation pressure	1	Rogers et al. (2016).
					High feeding rate	1	Rogers et al. (2016).
					High predator abundance	1	Rogers et al. (2016).
35.2	Rogers et al. (2016).	S1	*Botrylloides violaceus*	predators absent	Gregarious behaviour	1	Grey (2010).
					High fecundity	1	Bock et al. (2011).
					High recruitment	1	Grey (2010).
					High dispersal	0	Saito et al. (1981).
					Predation refuge	1	Rogers et al. (2016).
					Predation pressure	0	Rogers et al. (2016).
					High feeding rate	0	Rogers et al. (2016).
					High predator abundance	0	Rogers et al. (2016).
35.3	Rogers et al. (2016).	S4	*Didemnum vexillum*	various benthic predators (crabs, starfish, urchins)	Gregarious behaviour	1	Forrest et al. (2013).
					High fecundity	1	Forrest et al. (2013).

					High recruitment	1	Bullard et al. (2007).
					High dispersal	0	Fletcher et al. (2013).
					Predation refuge	0	Rogers et al. (2016).
					Predation pressure	1	Rogers et al. (2016).
					High feeding rate	1	Rogers et al. (2016).
					High predator abundance	1	Rogers et al. (2016).
35.4	Rogers et al. (2016).	S1	*Didemnum vexillum*	predators absent	Gregarious behaviour	1	Forrest et al. (2013).
					High fecundity	1	Forrest et al. (2013).
					High recruitment	1	Bullard et al. (2007).
					High dispersal	0	Fletcher et al. (2013).
					Predation refuge	1	Rogers et al. (2016).
					Predation pressure	0	Rogers et al. (2016).
					High feeding rate	0	Rogers et al. (2016).
					High predator abundance	0	Rogers et al. (2016).
35.5	Rogers et al. (2016).	S4	*Watersipora subtorquata*	various benthic predators (chitons, crabs, starfish, urchins)	Gregarious behaviour	1	Piola and Johnston (2009).
					High fecundity	1	Piola and Johnston (2009).
					High recruitment	1	Piola and Johnston (2009).
					High dispersal	0	Needles et al. (2015).
					Predation refuge	0	Rogers et al. (2016).
					Predation pressure	1	Rogers et al. (2016).
					High feeding rate	1	Rogers et al. (2016).
					High predator abundance	1	Rogers et al. (2016).
35.6	Rogers et al. (2016).	S1	*Watersipora subtorquata*	predators absent	Gregarious behaviour	1	Piola and Johnston (2009).
					High fecundity	1	Piola and Johnston (2009).

					High recruitment	1	Piola and Johnston (2009).
					High dispersal	0	Needles et al. (2015).
					Predation refuge	1	Rogers et al. (2016).
					Predation pressure	0	Rogers et al. (2016).
					High feeding rate	0	Rogers et al. (2016).
					High predator abundance	0	Rogers et al. (2016).
36	Sanford and Swezey (2008).	S1	*Tetraclita rubescens*	*Nucella emarginata*	Gregarious behaviour	1	Engle and Davis (1996).
					High fecundity	1	Sanford and Swezey (2008).
					High recruitment	1	Sanford and Swezey (2008).
					High dispersal	1	Sanford and Swezey (2008).
					Predation refuge	1	Sanford and Swezey (2008).
					Predation pressure	0	Sanford and Swezey (2008).
					High feeding rate	0	Sanford and Swezey (2008).
					High predator abundance	1	Sanford and Swezey (2008).
37	Shinen et al. (2009).	S3	*Mytilus galloprovincialis*	*Nucella ostrina, Pisaster ochraceus, Cancer antennarius*	Gregarious behaviour	1	Liu et al. (2012).
					High fecundity	1	de Greef et al. (2013)
					High recruitment	1	Branch and Steffani (2004).
					High dispersal	1	McQuaid and Phillips (2000).
					Predation refuge	0	Shinen et al. (2009).

					Predation pressure	1	Shinen et al. (2009).
					High feeding rate	0	Shinen et al. (2009).
					High predator abundance	1	Shinen et al. (2009).
38.1	Simkanin et al. (2013). rocky reefs	S4	*Botrylloides violaceus*	various benthic predators (crabs, starfish, flatworms, fish, nudibranchs)	Gregarious behaviour	1	Grey (2010).
					High fecundity	1	Bock et al. (2011).
					High recruitment	1	Grey (2010).
					High dispersal	0	Saito et al. (1981).
					Predation refuge	0	Simkanin et al. (2013).
					Predation pressure	1	Simkanin et al. (2013).
					High feeding rate	1	Simkanin et al. (2013).
					High predator abundance	1	Simkanin et al. (2013).
38.2	Simkanin et al. (2013). floating structures	S1	*Botrylloides violaceus*	predators absent	Gregarious behaviour	1	Grey (2010).
					High fecundity	1	Bock et al. (2011).
					High recruitment	1	Grey (2010).
					High dispersal	0	Saito et al. (1981).
					Predation refuge	1	Simkanin et al. (2013).
					Predation presure	0	Simkanin et al. (2013).
					High feeding rate	0	Simkanin et al. (2013).
					High predator abundance	0	Simkanin et al. (2013).
39	Simoncini and Miller (2007).	S1	*Botrylloides violaceus*	*Strongylocentrotus droebachiensis*	Gregarious behaviour	1	Grey (2010).
					High fecundity	1	Bock et al. (2011).
					High recruitment	1	Grey (2010).
					High dispersal	0	Saito et al. (1981).
					Predation refuge	0	Simoncini and Miller (2007).
					Predation pressure	0	Simoncini and Miller (2007).

					High feeding rate	1	Simoncini and Miller (2007).
					High predator abundance	1	Simoncini and Miller (2007).
40	Troost (2010).	S2	*Crassostrea gigas*	various generalist predators (shore birds, fish, benthic predators)	Gregarious behaviour	1	Reise et al. (2017).
					High fecundity	1	Helm et al. (2004).
					High recruitment	1	Diederich (2005).
					High dispersal	1	Reise et al. (2017).
					Predation refuge	1	
					Predation pressure	0	Troost (2010).
					High feeding rate	1	Troost (2010).
					High predator abundance	1	Troost (2010).
41	Weerman et al. (2014).	S2	*Crassostrea gigas*	*Crangon crangon*	Gregarious behaviour	1	Reise et al. (2017).
					High fecundity	1	Helm et al. (2004).
					High recruitment	1	Diederich (2005).
					High dispersal	1	Reise et al. (2017).
					Predation refuge	1	Weerman et al. (2014).
					Predation pressure	0	Weerman et al. (2014).
					High feeding rate	1	Weerman et al. (2014).
					High predator abundance	1	Weerman et al. (2014).
42	Wilkie and Bishop (2012).	S2	*Crassostrea gigas*	*Morula marginalba*	Gregarious behaviour	1	Reise et al. (2017).
					High fecundity	1	Helm et al. (2004).
					High recruitment	1	Diederich (2005).
					High dispersal	1	Reise et al. (2017).
					Predation refuge	0	Wilkie and Bishop (2012).
					Predation pressure	0	Wilkie and Bishop (2012).

					High feeding rate	0	Wilkie and Bishop (2012).
					High predator abundance	1	Wilkie and Bishop (2012).
43	Skein (2019).	S2	*Semimytilus algosus*	*Marthasterias africana, Burnupena* spp., *Jasus lalandii*	Gregarious behaviour	1	Liu et al. (2012).
					High fecundity	1	Zeeman et al. (2018).
					High recruitment	1	Zeeman et al. (2018).
					High dispersal	1	Narváez et al. (2006).
					Predation refuge	1	Chapter 1, Appendix 5.2
					Predation pressure	0	Chapter 2,3
					High feeding rate	1	Appendix 1
					Large predator abundance	1	Chapter 2,3

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Appendix 5.2

Studies undertaken to fill research gaps related to the invasion of *Semimytilus algosus* in subtidal communities along the South African coastline.

Growth rates of subtidal mussels

Prey such as mussels cannot actively escape from predators and must therefore rely on different strategies to escape predation. Mussel predators are often size selective (Creswell and McLay 1990; Griffiths and Seiderer 1980; Juanes 1992) and therefore species that can grow rapidly to the size beyond which they no longer represent an ideal prey choice for predators would have an advantage over those prey with slower growth rates. Information regarding the growth rate of subtidal *Semimytilus algosus* in comparison to co-occurring native subtidal mussels *Aulacomya atra* and *Choromytilus meridionalis* was therefore required to inform this important life-history strategy.

Individuals of the three subtidal mussel species (*A. atra*, *C. meridionalis*, and *S. algosus*) with shell lengths of 20 – 30 mm were collected at the same sites as described in Chapter 3 (n = 100 for each species). The shells of all mussels were notched at the posterior-ventral margin with a triangular file without damaging any living tissue and then measured with Vernier callipers to the nearest 0.1 mm, representing the initial length (Fig. 5.2.1). Mussels were subsequently transported to False Bay Yacht Club in Simons Town where they were placed into one of two cages with sides measuring 25 x 25 cm (n = 50 per species per cage). Cages were suspended with ropes from the walkons to a depth of 3 m and retrieved after a period of two months. Final lengths of mussels were taken as the distance from the umbo to the ventral margin of the shell, representing the growth increment (Fig. 5.2.1).

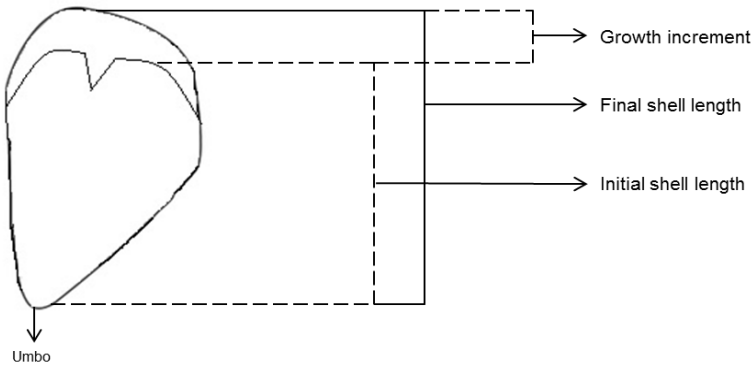

Figure 5.2.1: Illustration of the way mussel growth was measured. Initial length is represented by the distance from the umbo to the posterior-ventral shell margin, while the final length was the distance from the umbo to the posterior shell margin after three months. The growth increment is the difference between these two distances.

For each species, Ford-Walford plots were derived via a regression of the final shell length to the initial shell length using the regression equation,

$$L_{t+2\,\text{months}} = mL_{t0} + i$$

where L_{t0} represents the initial length, $L_{t+2\,months}$ the final shell length, m the slope, and i the intercept on the y-axis (Steffani and Branch 2003). For bivalve taxa, von Bertalanffy growth curves are used, and were calculated here using the constants derived from the Ford-Walford plots. These growth curves are calculated using the equation,

$$L_t = L_\infty (1 - e^{-Kt})$$

where L_t represents the length at age t, and L_∞ the asymptotic length, determined by $i/(1-m)$ from the Ford-Walford plot. The growth coefficient K was determined by the growth over the 2-month timeframe and is calculated from $-\ln m$ (Steffani and Branch 2003). Although studies of other mussel species have found seasonal growth patterns (Hemachandra and Thippeswamy 2008), such effects are assumed not to be influential in this study system. This is due to the fact that food supply and temperature along this stretch of coastline remain fairly constant throughout the year (Bustamante and Branch 1996) and has been validated in intertidal studies (Steffani and Branch 2003; Xavier et al. 2007). Differences in growth rates between species were analysed by comparing the slopes of the Ford-Walford growth regressions through an ANCOVA.

The slopes of these regressions differed significantly ($F_2 = 316.6$, $p < 0.001$), and was influenced by mussel species ($F_2 = 330.51$, $p < 0.001$) and initial length ($F_1 = 557.85$, $p < 0.001$)

(Fig. 5.2.2a). The interaction between these two factors was also significant (F_2 = 7.531, p <0.001). A Tukey post hoc test revealed that the slope of *C. meridionalis* was significantly smaller compared to the slopes of *A. atra* (p = 0.001) and *S. algosus* (p = 0.01), while the slopes of *A. atra* and *S. algosus* did not differ. However, note that the intercept of *A. atra* is smaller than that of *S. algosus*, indicating a smaller size in the former. This is further supported by the von Bertalanffy growth curves (Fig. 5.2.2b) and relative asymptotic lengths of the species (Table 5.3). Notably, *S. algosus* has a large asymptotic length (L_∞) compared to native species, although the small growth coefficient (K) of *S. algosus* suggests that it would take longer for this species to reach L_∞. (Table 1, Fig. 5.2.2b).

Table 5.2.1: Constants of the Ford-Walford growth regressions (m – slope, i – intercept, r^2 – coefficient of determination) and von Bertalanffy growth curves (K – growth coefficient for growth over 2 months, L_∞ - asymptotic length (mm)).

Mussel species	**Ford-Walford**			**von Bertalanffy**	
	m	i	r^2	K	L_∞
Aulacomya atra	0.93248	3.7574	0.79	0.069	55.65
Choromytilus meridionalis	0.47	31.79	0.21	0.755	59.981
Semimytilus algosus	0.8491	17.12	0.31	0.164	113.45

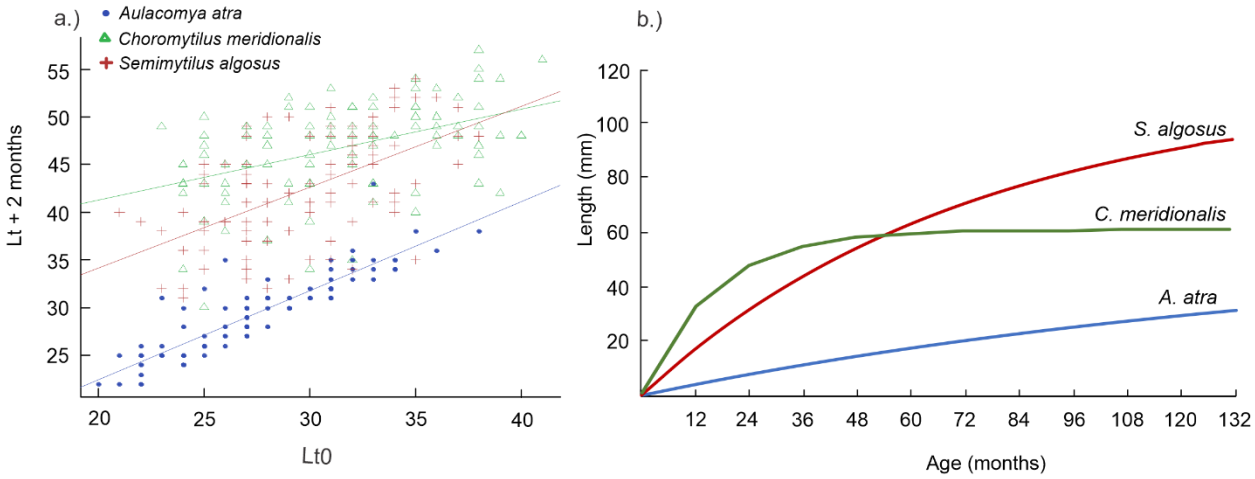

Figure 5.2.2: a) Ford-Walford regressions of the initial (L_{t0}) to the final ($L_{t\,+\,2\ months}$) length of *Aulacomya atra*, *Choromytilus meridionalis*, and *Semimytilus algosus*. b.) von Bertalanffy growth curves of *A. atra*, *C. meridionalis*, and *S. algosus*.

The high growth rate and asymptotic size of *S. algosus* in the subtidal zone suggests that not only can this species escape the 'window of vulnerability' of predation, it will likely reach this refuge before co-occurring native mussels *A. atra* and *C. meridionalis*. Mussels are likely faced with energetic trade-offs between investment toward growth rates and shell thickness. The native *A. atra* has the thickest shells out of the three subtidal mussel species examined (Chapter 2), which may explain its slow growth and smaller asymptotic size (Zeeman et al. 2018). Indeed, this species is well-known for having slow growth rates (van Erkom Schurink and Griffiths 1993). An unexpected finding was the relatively short asymptotic length of *C. meridionalis*, as this native mussel has been found in much larger sizes from subtidal environments (Chapter 1). A potential explanation for this could be the densities in which co-occurring species were present, especially *S. algosus*. Although not explicitly examined, it is possible that *S. algosus* may have smothered the native species in the growth cages, which could reduce their feeding rates and thereby indirectly their growth rates. Indeed, mussels have been found to grow to larger sizes when densities were low (Xavier et al. 2007). This would, however, need to be verified in future research.

The results gained from this experiment are in sharp contrast to what has been reported from intertidal habitats. In a recent study by Zeeman et al. (2018), the asymptotic length of *S. algosus* was much smaller (52.89 mm) than reported here (113.45 mm) and this species also had the slowest growth rate out of those that were examined. It has been suggested that in intertidal habitats, *S. algosus* can likely compensate for its slow growth through high recruitment rates (Zeeman et al. 2018). There are several key environmental differences between intertidal and subtidal habitats. Tidal cycles, wave exposure and temperature variations have strong effects on the life-history characteristics of intertidal mussels (Branch et al. 2010; van Erkom Schurink and Griffiths 1993), while these variables are absent from subtidal environments. Different growth rates between intertidal and subtidal species should therefore perhaps not be surprising, although it emphasizes the scale in which important life-history characteristics of species can differ between these environments.

A potential drawback of this experiment is that growth was measured at a single, relatively sheltered subtidal site within a bay. This could be improved in the future by inlcuding more sites and exposures. Mussel growth rates on the South African coastline have indeed been shown to vary over a degrees of exposure (Steffani and Branch 2003) and upwelling intensities (Xavier et al. 2007). Overall, the comparatively slower growth rates and smaller sizes of native mussels will

likely render these species more susceptile to strong predation from subtidal predators in comparison to the fast growing and larger invasive *S. algosus*.

Functional responses of *Jasus lalandii* feeding on different mussel prey

Predator functional responses (FRs), the rate of prey consumption in relation to prey density (Holling 1959), are increasingly being applied in invasion ecology to not only predict the impacts of invasive predators on native prey populations, but also to predict the potential regulatory forces of native predators on invasive prey (Cuthbert et al. 2018; Joyce et al. 2019). Predators that demonstrate a type II FR (destabilizing) will exhibit high feeding rates on prey offered at low densities (Hassell 1978). Those that forage according to a type III FR (stabilizing) will only start to exhibit high feeding rates as prey densities start to increase, thus offering prey a low-density refuge (Murdoch and Oaten 1975). As such, for native predators to effectively resist the establishment or further spread of an invasive prey species, they would need to forage according to a type II FR.

Three native predators have been considered throughout this study: the starfish *Marthasterias africana* (Chapter 2), *Burnupena* whelks (Chapter 3), and rock lobsters *Jasus lalandii* (Chapter 2, 3, and 4). Besides showing an active avoidance of *S. algosus* (Chapter 2 and 3), starfish and whelks naturally have slow feeding rates. Rock lobsters, on the other hand, have exceptionally high feeding rates (personal observation) and have shown flexible prey selection throughout experiments conducted throughout this thesis. As such, a laboratory experiment was conducted to establish if *J. lalandii* exhibits a type II FR when feeding on *S. algosus*, and to compare this with the feeding responses towards native mussels that co-occur with *S. algosus* in subtidal habitats (*A. atra* and *C. meridionalis*).

Rock lobsters (70 – 120 mm carapace length) were collected from Sea Point on the Atlantic Seaboard of the Cape Peninsula (33º55’13’’S, 18º22’48’’E) and brought to the laboratory. Individual lobsters were kept in 38l tanks in aerated seawater (13ºC) and allowed to acclimatize for 48 hours prior to experiments. Lobsters were not fed during this time. Mussels (20 – 30 mm) were collected from the same sites as described in Chapter 2. The FRs of *J. lalandii* when feeding on the various prey species was examined through presenting individual rock lobsters with different densities of each prey species in isolation (densities: 3, 6, 9, 12, and 15).

There were three replicates per density per prey species, resulting in a total of 45 trials. Trials lasted for 24 hours and mussels were not replaced upon consumption. It was not possible

to use a new lobster for each trial given permit regulations that prohibited additional collections of rock lobsters from the field. As such, some individuals had to be reused. Care was taken to ensure that no single lobster was exposed to the same mussel species more than once and a starvation period of 24 hours was applied after each trial.

FR types was determined through a logistic regression of the proportion of prey consumed as a function of prey density (Juliano 2001). A type II FR can be assigned when the first order term is significantly negative, while a type III FR can be assigned when the first order term is significantly positive, followed by a significantly negative second order term. FR analyses were undertaken using the 'frair' package in R (Pricthard et al. 2017). A type II Rogers' random predator equation was fitted to the data to account for prey depletion (Juliano et al. 2001):

$$N_e = N_0\big(1 - \exp\big(a(N_e h - T)\big)\big),$$

Where N_e represents the number of prey eaten, N_0 is the initial density of the prey while a represents the attack constant, h handling time and T the total experimental period. The 'Lambert W' function was subsequently used for model fitting and to generate bootstrapped data (n = 1000) with 95% confidence intervals.

Survival of all mussels in the holding tanks confirmed that mortality in treatments was due to predation and no other confounding factors. Rock lobsters displayed significant type II (destabilizing) FRs when feeding on each mussel species (Table 5.2.2).

Table 5.2.2: Results of the logistic regression for type II FR (1st term and associated p-value) of *Jasus lalandii* feeding on *Aulacomya atra*, *Choromytilus meridionalis*, and *Semimytilus algosus* and parameter estimates (a = attack rate, h = handling time with associated p-values).

Prey species	**Type II FR**	**Parameter estimates**	
	1st term	a	h
Aulacomya atra	- 0.064 (p < 0.001)	1.697 (p < 0.01)	0.109 (p < 0.001)
Choromytilus meridionalis	- 0.098 (p < 0.001)	2.627 (p < 0.001)	0.106 (p < 0.001)
Semimytilus algosus	- 0.078 (p < 0.001)	2.832 (p < 0.01)	0.092 (p < 0.001)

The confidence intervals of the FR curves for all prey species overlapped across all densities (Fig. 5.2.3), indicating no significant differences in parameter estimates such as attack rate and handling time.

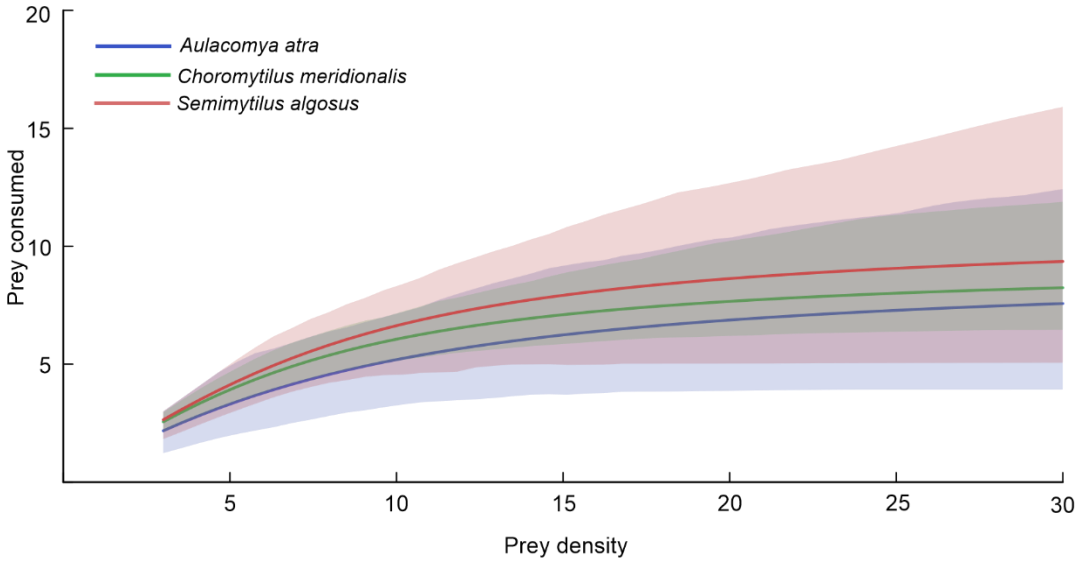

Figure 5.2.3: Functional response of *Jasus lalandii* feeding on three prey species: native *Aulacomya atra* (blue), *Choromytilus meridionalis* (green), and invasive *Semimytilus algosus* (red). Data are mean prey consumed at increasing prey densities with bootstrapped (n = 1000) 95% CIs.

The fact that *J. lalandii* displays a type II FR when feeding on mussel prey confirms the important influence of this subtidal predator on prey populations. However, the fact that there is no significant difference in feeding rates on the three prey species indicates that *S. algosus* will not be consumed faster than native mussels. This finding, in conjunction with the avoidance of *S. algosus* reported in Chapter 2, suggests that rock lobsters are unlikely to have strong impacts on populations of *S. algosus* in subtidal communities where alternative native prey is present.

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